An Evaluation of the SAK Model as Applied in Wisconsin

To:

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1.0 Executive Summary

The Sex-Age-Kill (SAK) model has been used for estimation of white-tailed deer populations in Wisconsin since the 1960s. Despite the long history of SAK model use, population estimates have been questioned by sporting groups, including the Wisconsin Conservation Congress, which has led to questions about the validity of the SAK model. This project was undertaken to critically review and better understand the potential biases in the SAK model as applied in Wisconsin. Our goal was to improve the understanding and utility of SAK estimates by investigating structural issues, model assumptions, the validity of model inputs, and the procedural issues involving SAK use in Wisconsin.

Following a day-long meeting with the Wisconsin Department of Natural Resources, the Wisconsin Conservation Congress, and other interested parties, panel members identified the following tasks: (1) Evaluate the impact of the assumption of a stable and stationary population for pre-and post-hunt population estimates; (2) Investigate issues of precision at the local (DMU) level including an evaluation of the uncertainty and precision of the estimates; (3) Evaluate key assumptions of the SAK model and their influence on population estimates; (4) Investigate the possibility of adding auxiliary information in the SAK model; (5) Evaluate issues identified by the Conservation Congress and other interested parties; (6) Evaluate adjustments made in the model by DNR personnel; and (7) Complete a literature review to investigate the availability of alternative monitoring and evaluation techniques and investigate what other states do to monitor deer populations.

We used a combination of computer simulations, demographic modeling, literature reviews, and surveys to complete our tasks. In doing so, we investigated sources of systematic bias, deterministic and stochastic effects on SAK performance; evaluated the precision of SAK estimates; compared the SAK with other techniques including the Lang and Wood (1976) and Downing (1980) methods; evaluated the appropriateness of adjustments made by DNR personnel including the buck recovery rate and fawn:doe ratios and whether those adjustments could be made more objectively; completed a review of alternative population estimation methods and a review of how other state agencies monitor deer populations; and evaluated the performance of running averages of the male and female yearling proportions to determine whether they improve SAK performance. Based on our evaluation, we offer the following conclusions:

(1) Wisconsin has the most comprehensive and transparent deer management program for comparable states that harvest white-tailed deer. Wisconsin collects more demographic information, on an annual basis, to monitor the deer population than any of the 21 states we surveyed. The WDNR should be commended for its efforts to track deer population dynamics and make those efforts transparent.

(2) There are several positive aspects of the SAK model as it is applied in Wisconsin. First, the model does reasonably well at estimating N_i (estimate of deer abundance immediately before the *i*th hunting season) at the state-wide level. Second, the model appears relatively robust to changes in female harvest. Third, when the population is nonstationary (i.e., population increasing or decreasing in size) with a stable age distribution, there is only minor bias in

population estimates. Last, the model allows for an extensive population assessment in contrast to more expensive and intensive procedures.

(3) The SAK model appears to be very sensitive to sudden changes in the male harvest rate. We noted wide changes in SAK estimates compared with simulated known populations as a result of changing male harvest rates. Perhaps most troubling is that the SAK estimates are opposite the true population trend when changes in the male harvest rate are introduced. Given these findings, any change in regulations that alters the male harvest rate (e.g., earn-a-buck) could bias population estimates. Changes in hunter attitude and hunting styles, such as quality deer management, could further adversely affect SAK estimates given its sensitivity to male harvest rate.

(4) The scale of estimation is important and must be considered when evaluating SAK performance. SAK estimates may be precise at the state level, but less so at the DMU level. When both demographic stochasticity and sampling error are considered at DMU levels, the resultant abundance estimates were within $\pm 121.9\%$ of the true population level, 95% of the time. The SAK model is particularly vulnerable to model violations because of the focus on one age class (1.5 year olds).

(5) The methods previously used to evaluate the ability of the SAK model to predict future harvests (WDNR 2001) are inappropriate because they do not directly relate to the same scale at which management decisions are made. For 16 DMUs examined, the SAK model explained up to 62% of the variability in the relationship between predicted versus actual harvests among years. However, for some DMUs, the SAK model does a poor job of predicting future harvests. In light of these findings, we recommend that any evaluation of the predictive capabilities of the SAK model be applied to individual DMUs over time rather than across DMUs. Special attention should be paid to understanding deer harvests and populations in those DMUs where the SAK model predicts poorly over time because it might provide insight for improving deer population modeling in Wisconsin.

(6) In northern Wisconsin, precision of the population's finite rate of increase ($\hat{\lambda}$) is not adequate for precise projections from N_i to N_{i+1} (a projection of N_i to the next hunting season). The precision of N_{i+1} is inherently low because of variability in $\hat{\lambda}$. The rest of Wisconsin does not have a formal model to estimate $\hat{\lambda}$. Hence, we were unable to determine the precision or bias due to $\hat{\lambda}$ for the rest of the state. There is a great need to better understand the factors that influence the abundance of deer for the upcoming hunting season.

(7) Occasionally WDNR pools data spatially and temporally for input into the SAK model. Spatial pooling is valid if demographic processes across pooled units are homogenous (meaning that sex and age composition, S_N [the probability of natural survival], S_H [the probability of surviving harvest], and $\hat{\lambda}$ are all the same). Pooling and substituting data is a matter of convenience, providing cost savings and improvements to precision because of increased sample sizes; however, there are risks of additional bias if the population is not stable and stationary.

(8) Precision expressions for SAK estimates are currently unattainable given the data input used in the model. Without empirical estimates of all inputs, it is not possible to calculate confidence intervals. Currently, we only have empirical estimates for the following parameters: $\hat{p}_{YM}$ (the proportion of 1.5 year old males in the adult buck segment of the population), $\hat{p}_{YF}$ (proportion of 1.5 year old females in the adult female segment of the population), $\hat{R}_{J/F}$ (estimated ratio of juveniles to adult females in the population), and $\hat{\lambda}$ for the northern forested region, but not elsewhere. We do not have empirical estimators or the ability to estimate the variance of the following inputs: θ (the sex ratio of fetal males:juveniles from McCaffery et al. [1998]), $\hat{B}$ (proportion of total annual mortality of adult males associated with sport harvest, termed the buck recovery rate), and H_i (estimated adult buck harvest in year i). If statistically rigorous measures of precision are desired for population estimates by DMU, the following data are required: harvest reporting rate, buck reporting rate, and wounding loss rate. Even if the average number of deer from the antlered and antlerless harvests that were aged each year (in each DMU) did not change, more consistency in the number of deer aged from year to year could potentially reduce the variability in the precision of population estimates.

(9) Expressing SAK estimates as density based on "available deer range" adds another source of variability, which is important when conveying modeling results to the public. When expressing SAK estimates as density, it requires that available deer range be defined and precisely estimated. There is an inherent patchiness in deer range, which likely confuses the public. In addition, variable harvest pressure can affect density distribution. Reporting deer abundance as total numbers (e.g., there are 10,131 deer in a DMU) rather than deer density (e.g., there are 30 deer per square mile) minimizes problems with public concern when local abundance appears to deviate from reported densities. It would be advisable to provide SAK abundance estimates rather than density.

(10) The running averages of p_{YM} and p_{YF} produced marginal improvement of SAK performance. Despite only modest improvements to SAK performance, we recommend continued use of running averages, which is necessary because of the highly variable number of deer that are aged each year. Furthermore, we recommend the use of a weighted average.

(11) Given currently available data, it is not possible to make objective adjustments to $\hat{B}$. Given $\hat{B}$ is based on history and intuition without any empirical basis, it is not possible to set criteria or objective rule statements. We recommend $\hat{B}$ be estimated through field studies involving radiotelemetry studies under diverse deer densities, hunter density, number of days hunted, percentage of land accessible to hunters, and weather conditions prior to and during the hunting season.

(12) Including July data in the fawn:doe ratio estimates will negatively bias results because does are still hiding fawns by early July. Therefore only August and September data should be used to estimate $\hat{R}_{J/F}$. Also, the sampling scheme for obtaining these data has potential for bias, for example, it is easiest to obtain a sample in localities with highest density. We recommend that a systematic scheme producing reasonable coverage be considered. We also recommend WDNR

initiate an analysis of the extent of variation in fawn:doe ratios and an evaluation of alternative sampling schemes.

(13) We reviewed seven alternative methods to the SAK model as potential methods for estimating deer abundance in Wisconsin. Six of those methods are unlikely to provide more accurate and precise estimates than the SAK model because it is unlikely that critical assumptions of the techniques can be met. Unrealistic assumptions required in the SAK model might be eliminated if auxiliary data were collected to estimate age- and sex-specific harvest rates. However, these data also could also be used in alternative estimation methods, such as the statistical age-at-harvest approach (e.g., Gove et al. 2002), which might hold promise for deer estimation in Wisconsin.

(14) The combination of multiple data sources, both extensive and intensive might allow for a more rigorous demographic assessment. The relative trade-off between these broad and fine scale methods should be investigated in light of WDNR monitoring objectives. The costs of collecting sufficient data to obtain a statistical measure of precision for all DMUs using Wisconsin's SAK model are likely prohibitively expensive or even logistically impossible. Cost comparisons between the SAK and other population estimation techniques would be beneficial and should be performed. Reconstruction methods such as the SAK provide a cost effective method for broad-scale demographic assessments.

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2.0 Introduction

Estimating the number of white-tailed deer (*Odocoileus virginianus*) in Wisconsin has been controversial for many years. In 1943 Aldo Leopold estimated the Wisconsin deer population at 500,000 animals. His estimate was questioned by Roy Jorgensen, editor of "*Save Wisconsin's Deer*" who instead suggested there were 200,000 deer. More recently, the Wisconsin Conservation Congress initiated efforts to evaluate the credibility of deer population estimates. Among the recommendations made in their "*Final Report of the Believability of DNR White-tailed Deer Population Estimates*" report, the Wisconsin Conservation Congress suggested that an outside audit be performed to evaluate the scientific credibility of the SAK population estimation model. This study was undertaken to critically review and better understand the potential biases in the SAK model as applied in Wisconsin.

3.0 Background

Wisconsin's white-tailed deer population management program is based on a system of deer management units (DMUs) with established population density goals. Annual population estimates are compared to goal densities and quotas for antlerless deer harvests are developed to meet those population goals. Antlerless harvest recommendations are based on the predicted size of fall populations. Fall herd size is predicted using estimated post-hunting-season population estimates and predicted rates of population increase.

Historically, annual population estimates in Wisconsin have been based on pellet-group counts, deer-trail surveys, and Sex-Age-Kill (SAK) estimates. Pellet-group counts were discontinued in 1978 and the use of deer-trail surveys stopped in 1983 because of high labor requirements. In the 1960s, the Wisconsin DNR began using the Sex-Age-Kill (SAK) procedure. The SAK procedure was first developed by the Michigan Department of Conservation

(Eberhardt 1960). The technique assumes that the total buck harvest is a reliable index of the prehunt population size. The SAK model is one variant in a larger family of population assessment models (Lang and Wood 1976, Skalski et al. 2005). Variations of the SAK model have been used to estimate white-tailed deer and other wildlife abundance (e.g., black bears [*Ursus americanus*], black-tailed deer [*Odocoileus hemionus*] in Washington state) by numerous wildlife management agencies (Creed et al. 1984, Skalski and Millspaugh 2002, Skalski et al. 2005). The model relies on age-at-harvest data that are routinely collected by wildlife management agencies. When compared with other methods, the technique is cost efficient and has been reported to provide a good index of deer abundance when all age- or size-classes of antlered deer are harvested at the same rate (Creed et al. 1984, Hansen 1998).

In Wisconsin, SAK estimates combine data on the following: (1) the size of unit-specific deer harvests, based on mandatory registration of all harvested deer; (2) age and sex composition of harvested deer; and (3) fawn:doe ratios to calculate population estimates for each management unit. The SAK model assumes that the age-composition of harvested bucks (1.5+ years old) is an accurate measure of the age-composition of the living adult male population (i.e., there is no age-related selection bias). The Burgoyne method (Burgoyne 1981) is used to estimate the annual mortality rate of adult bucks from the harvest age-composition. Annual mortality rates are converted to estimates of harvest mortality rates by dividing the annual mortality rate by an approximation for the percentage of adult males that die due to legal hunting, termed the buck recovery rate. The size of the adult male population prior to the hunting season is estimated by dividing the number of harvested bucks by the estimated harvest rate. Estimated buck:doe ratios and fawn:doe ratios are then used to expand the adult male population size to estimate the total population.

The fawn:doe ratios used in the SAK population model are based on observations of deer during July, August, and September by DNR personnel during normal duty travels. Due to sampling limitations, fawn:doe ratios are estimated for 13 groups of management units. For northern management units, annual observed ratios are used in the SAK model. Because of small annual samples in southern units, fixed constants are used in these units. The reliability and precision of fawn:doe ratios used in the SAK procedure have not been evaluated.

4.0 Goal

The goal of this technical review is to improve the understanding and utility of SAK estimates by investigating structural issues, model assumptions, the validity of model inputs, and the procedural issues involving SAK use in Wisconsin.

5.0 Approach and Tasks

On 30 September 2005, panel members (Mark Boyce, Duane Diefenbach, Lonnie Hansen, Kent Kammermeyer [via conference call], Joshua Millspaugh, and John Skalski) participated in an all-day meeting with Wisconsin Department of Natural Resources personnel, Conservation Congress representatives, and other interested parties to discuss the SAK model and its application in Wisconsin. Robert Rolley provided an extensive overview of the SAK model as applied in Wisconsin, an overview of deer harvest management in Wisconsin, and a discussion of data collection techniques.

The panel also heard from the Conservation Congress and other interested parties. The Conservation Congress identified several key issues of interest including the credibility of SAK estimates; the applicability of current SAK modeling given other available data and methods; appropriateness of the adjustments made by DNR personnel including the buck recovery rate (Appendix A) and fawn:doe ratios and whether those adjustments could be made more objectively; and whether confidence intervals could be provided for SAK estimates. The additional conversations Joshua Millspaugh had with Steve Oestricher and Ed Harvey (Conservation Congress) confirmed the issues identified at the September 2005 meeting.

Panel members outlined the general approach they expected to use to complete the review. An initial coordination plan was outlined. The following tasks were identified by panel members:

1. Evaluate the impact of the assumption of a stable age distribution and stationary population (i.e., constant abundance) for pre-and post-hunt population estimates.
2. Investigate issues of precision at the local (DMU) level including an evaluation of the uncertainty and precision of the estimates.
3. Evaluate key assumptions of the SAK model and their influence on population estimates.
4. Investigate the possibility of adding auxiliary information in the SAK model.
5. Evaluate issues identified by the Conservation Congress and other interested parties.
6. Evaluate adjustments made in the model by DNR personnel.
7. Complete a literature review to investigate the availability of alternative monitoring and evaluation techniques and investigate what other states do to monitor deer populations.

6.0 Topics of Investigation

There are four general areas of investigation within this report:

1. *Structural issues*. The SAK model uses a series of input variables to calculate a population estimate. All of the variables are estimated and have an associated variance and potential bias. These features affect estimates of precision for SAK estimates.

2. *Model assumptions.* Model assumptions include: (1) model inputs are estimated without bias, (2) the underlying model is deterministic, and (3) the population is stable and stationary (i.e., throughout the report we use "stable" to denote a population with a stable age distribution and "stationary" to indicate a population with constant abundance).

3. *Validity of model inputs.* There are six inputs to the SAK model (for N_i) estimation that are collected during the hunting season or estimated based on previous studies and data. These include:

- *Buck recovery rate*. This parameter represents the proportion of total buck mortality due to registered harvest. The SAK procedure as used requires that the annual buck harvest rate is constant from year to year for individual management units because harvest age structure data reflect past mortality rates, not the current season's mortality rate. Several factors discussed above could potentially affect annual variability in buck harvest rates.

- *Fawn:doe ratio*. The fawn:doe ratio data used in the SAK model are based on visual surveys. For some DMUs, annual estimates are unavailable.

- *Proportion of yearling bucks in the registered harvest*. This information is collected during the hunting season from a sample of bucks at registration stations throughout the state. The proportion of yearling bucks in the adult buck harvest is used as a measure of total annual buck mortality.

- *Adult sex ratio*. Proportions of yearling bucks and yearling does in the harvest and the pre-birth sex ratio are used to estimate the adult sex ratio.

- *Pre-birth sex ratio*. This information was collected in several different studies. The fetal sex ratio is assumed to be 100 females:110 males based on empirical data from 1,686 does examined in Wisconsin during 1982 – 1987 (McCaffery et al. 1998). No current work is being pursued to collect this information.

• *Total registered harvest collected through mandatory registration*. Since it is assumed that the harvest is known and complete from the registration, no variance can be estimated.

4. *Procedural Issues*. WDNR biologists have developed an *ad hoc* way of dealing with the uncertainty introduced to the model by the structural and assumption issues. For example, professional judgment is used by the deer committee in deciding whether to adjust the buck recovery rate in response to hunting season conditions, and when to update estimates of buck mortality rate and adult sex ratios. Further, staff effort limitations preclude collecting age, fawn:doe ratio, and sex ratio data in every deer management unit each year. Parameter estimates for some units are based on data for surrounding units taking into consideration habitat, hunting pressure, and season framework.

7.0 Quantitative Description of SAK Model

The SAK model uses in-season demographic information and expert opinion input to translate buck harvest into an estimate of total white-tailed deer abundance. The SAK calculations provide two abundance estimates; one is an estimate of deer abundance immediately before the *i*th hunting season (i.e., $\hat{N}_i$), the other is a projection of that abundance to the following hunting season (i.e., $\hat{N}_{i+1}$). This projection of next year's deer abundance is used in setting harvest regulations.

The fundamental equation for the SAK analysis (Skalski and Millspaugh 2002) is

$$\hat{N}_i = \hat{N}_M + \hat{N}_F + \hat{N}_J \tag{1}$$

where

$\hat{N}_i$ = estimate of total abundance in year i;

$\hat{N}_M$ = estimate of adult (1.5+ years of age) male abundance;

$\hat{N}_F$ = estimate of adult (1.5+ years of age) female abundance;

$\hat{N}_J$ = estimate of juvenile (< 1.5 years of age) abundance.

Using the ratios of adult female to adult male and juvenile to adult female, total abundance can be estimated as (Skalski and Millspaugh 2002)

$$\begin{aligned}\hat{N}_i &= \hat{N}_M + \hat{N}_M \cdot \hat{R}_{F/M} + \hat{N}_M \cdot \hat{R}_{F/M} \cdot \hat{R}_{J/F} \\ &= \hat{N}_M \left(1 + \hat{R}_{F/M} + \hat{R}_{F/M} \cdot \hat{R}_{J/F}\right),\end{aligned} \tag{2}$$

where

$\hat{R}_{F/M}$ = estimated ratio of adult females to adult males in the population;

$\hat{R}_{J/F}$ = estimated ratio of juveniles to adult females in the population.

The key to the SAK model is the estimate of adult male abundance based on harvest data, expressed as

$$\hat{N}_M = \frac{\hat{H}}{\hat{K}}, \tag{3}$$

where

$\hat{H}$ = estimated total harvest of adult males from the population;

$\hat{K}$ = estimated probability of harvesting an adult male.

The harvest probability, in turn, can be estimated by

$$\hat{K} = \hat{M}_T \hat{B}, \tag{4}$$

where

$\hat{M}_T$ = total annual mortality rate of adult males;

$\hat{B}$ = proportion of total annual mortality of adult males associated with sport harvest (buck recovery rate).

The buck recovery rate $(\hat{B})$ has no associated measure of precision and is modified, as needed based on expert opinion from Wisconsin DNR biologists, on an annual basis (Appendix A). An explanation of how the buck recovery rate was derived for use in Wisconsin's SAK model is provided in the *Management Workbook for White-tailed Deer* (WDNR 2001). The following formula has been created to describe the relationship between $\hat{B}$ and $\hat{p}_{YM}$ (the proportion of 1.5 year old males in the adult buck segment of the population) (R. E. Rolley, personal communication), although not all DMUs used this model-based estimate of $\hat{B}$:

$$\hat{B} = \frac{96.7}{100} \cdot \left[1 - \exp\left\{-(0.051 \cdot (\hat{p}_{YM} \cdot 100 - 31))\right\}\right]. \tag{5}$$

In Wisconsin, the harvest ($\hat{H}$) parameter in the SAK model is not estimated but used as a known value. This value is assumed to be known without error because all legally harvested deer are required to be presented at registration stations. Although a survey of state wildlife agency personnel reported strong confidence in data from registration stations, no states have reported any quantifiable measure of compliance rates with check stations and some states agencies have questioned the reliability of check station data (Rupp et al. 2000). Rosenberry et al. (2004) reported declining compliance rates with a mandatory mail-in report card harvest system even though the reporting system had not changed over several decades.

Combining Eqs. (2), (3), and (4) yields the SAK model, expressed as

$$\hat{N}_T = \frac{\hat{H}}{\hat{M}_T \hat{B}} \left[1 + \hat{R}_{F/M} + \hat{R}_{F/M} \cdot \hat{R}_{J/F}\right]. \tag{6}$$

This generic form of the SAK model [Eq. (6)] requires no specific assumptions concerning the structure of the population or its dynamics over time. This five-parameter model can be used for abundance estimation without loss of generality. However, to easily estimate some of the input parameters, an assumption of a stable and stationary population is invoked. In reality, the stationary assumption is difficult to reach. Ungulate populations could approach a stationary age distribution if there were strong density dependence keeping the population relatively constant (see Eberhardt 2002 and Owen-Smith 2006 for more information on density dependence in ungulates).

Based on the assumptions of a stable and stationary population, $\hat{M}_T$ can be estimated by the proportion $\left(\hat{p}_{YM}\right)$ of 1.5 year old males in the adult buck segment of the population (Burgoyne 1981). In this case, the SAK model can be expressed as

$$\hat{N}_i = \frac{\hat{K}}{\hat{p}_{YM}\hat{B}}\left[1+\hat{R}_{F/M}+\hat{R}_{F/M}\cdot\hat{R}_{J/F}\right]. \tag{7}$$

In the case of a stable and stationary population, the adult sex ratio can be estimated by

$$\hat{R}_{F/M} = \frac{\hat{p}_{YM}}{\hat{p}_{YF}}\cdot\hat{\theta}, \tag{8}$$

where

$\hat{p}_{YF}$ = proportion of 1.5-year-old females in the adult female segment of the population;

$\hat{\theta}$ = the sex ratio of fetal males:juveniles from McCaffery et al. (1998).

Primarily as a way to increase sample size and minimize the variability that occurs among annual estimates of this ratio, Wisconsin uses a five-year running average to estimate $\hat{p}_{YM}$ and $\hat{p}_{YF}$. This average proportion is calculated in different ways depending on the sample sizes of available data. If the number of deer aged in each of the five years is >50, the following formula is used:

$$\bar{\hat{p}}_k = \frac{1}{5}\sum_{i=1}^{5} \hat{p}_k \ ,$$

where $k = YM$ or YF. However, if in any year <50 deer are aged, a different formula is used:

$$\bar{\hat{p}}_k = \frac{\sum_{i=1}^{5} y_k}{\sum_{i=1}^{5} x_k} = \frac{\sum_{i=1}^{5} \hat{p}_k \cdot x_k}{\sum_{i=1}^{5} x_k}, \tag{9}$$

where x_k is the number of deer aged and y_k is the number of yearlings aged. It should be noted that the second formula is the preferred method of estimating $\hat{p}_{YM}$ and $\hat{p}_{YF}$, regardless of sample size in any given year, because each annual estimate is weighted by the total number deer aged.

Combining Eqs. (7) and (8) yields the final form of the SAK model, where deer abundance during the current year (N_i) is estimated by the formula

$$\hat{N}_i = \frac{\hat{H}_i}{\hat{p}_{YM}\hat{B}}\left[1 + \frac{\hat{p}_{YM}}{\hat{p}_{YF}} \cdot \hat{\theta} + \frac{\hat{p}_{YM}}{\hat{p}_{YF}} \cdot \hat{\theta} \cdot \hat{R}_{J/F}\right], \tag{10}$$

where

$\hat{H}$ = estimated adult buck harvest in year i, including wounding losses;

$\hat{B}$ = estimated adult buck recovery rate (i.e., proportion of total buck mortality due to harvest);

$= \dfrac{(1 - S_H)}{(1 - S_H \cdot S_N)}$, where S_N is the probability of natural survival (i.e., nonharvest sources of mortality), and S_H is the probability of surviving harvest;

$\hat{p}_{YM}$ = estimated proportion of 1.5-year-old bucks among adult bucks in the population;

$\hat{p}_{YF}$ = estimated proportion of 1.5-year-old does among all adult does in the population;

$\hat{\theta}$ = estimated sex ratio of juvenile males:juvenile females entering the adult age class;

$\hat{R}_{J/F}$ = estimated ratio of fawns (0.5-year-old males and females) to does (1.5+ year-old females) in the population.

The assumptions of the SAK abundance estimator $\hat{N}_i$ include the following:

1. Sample surveys provide unbiased estimates of the input parameters (i.e., H, B, p_{YM}, p_{YF}, θ, and $R_{J/F}$) in year i.
2. The deer population has a stable age distribution (i.e., constant sex and age-class proportions) and is stationary (i.e., constant abundance).

The latter assumption is necessary for $\hat{p}_{YM}$ to estimate the total annual mortality probability for bucks (Skalski et al. 2005:185-186) without bias and $\hat{p}_{YM} / \hat{p}_{YF}$ to estimate the adult sex ratio (Skalski et al. 2005:76-82).

The projected deer abundance to year $i+1$ is based on Eq. (10), adjusting for harvest losses and annual population growth, where

$$\hat{N}_{i+1} = \left(\hat{N}_i - \widehat{TH}_i\right)\hat{\lambda}_i, \tag{11}$$

and where

$\hat{\lambda}_i$ = estimated postharvest - prehunt lambda or estimate of the population growth quotient from one year to the next;

TH_i = total harvest across all age classes and genders in year i, including wounding losses.

The assumptions of $\hat{N}_{i+1}$, based on Eq. (11), include all those assumptions associated with estimating $\hat{N}_i$ plus the need for an accurate projection of population growth to the next year. In the Northern Forest region, Wisconsin, $\hat{\lambda}_i$ is estimated from a historical regression relationship between $\hat{\lambda}_i$ and a winter severity index (WDNR 2001:7.9).

8.0 Sources of Systematic Bias

The SAK model for estimating N_i has six input values whereas the SAK model for N_{i+1} has seven. Each of the values possesses uncertainty (but this uncertainty is not necessarily estimated), and each contributes to the overall uncertainty in the abundance estimates. Systematic error, where an input parameter is routinely or unintentionally estimated too large or too small, will contribute bias to the SAK estimates. This section examines the nature of the bias when input parameters to the SAK model are incorrect.

8.1 Estimate of Harvest $(\hat{H}_i)$

The bias in the SAK estimates of N_i and N_{i+1} is directly related to bias in the harvest estimates. Underestimation of H_i will result in an underestimation of total population abundance both in year i (i.e., N_i) and year $i+1$ (N_{i+1}). Buck harvest may be underestimated if segments of the hunting population fail to report their take.

8.2 Estimate of Buck Recovery Rate $(\hat{B})$

Bias in the SAK estimates (N_i and N_{i+1}) is inversely related to bias in the estimates of buck recovery rate (B). Should the overall contribution of harvest to total buck mortality be assumed too high, the resulting SAK estimates (i.e., N_i and N_{i+1}) will be biased downward. Conversely, should the buck recovery rate (B) be assumed lower than it truly is, then the SAK estimates will be positively biased, i.e., too high.

Harvest regulations, hunting conditions, hunter selectivity, as well as natural mortality (i.e., $1 - S_N$), all can affect the buck recovery rate (B) (Roseberry and Klimstra 1974, Roseberry and Woolf 1991). Therefore, values of B may be expected to change from one year to the next.

Consistent over- or underestimation of B could have long-term consequences on the deer abundance estimates.

8.3 Estimate of Juvenile Sex Ratio $(\hat{\theta})$

Wisconsin Department of Natural Resources (WDNR) (2001:6.6) adjusts the SAK model "to account for an unbalanced sex ratio at birth, assuming this imbalance persists through the 18 months of life." In actuality, $\hat{\theta}$ is the sex ratio of yearlings at the time of recruitment into the adult population. The value of $\hat{\theta}$ may not be 1, due to an unequal birth rate (Verme 1983, Hoefs and Nowlan 1994, DeYoung et al. 2004) or due to unequal natural survival (S_N) (Vreeland 2002) or juvenile harvest mortality (i.e., $1 - S_H$) (Nixon 1971) until 1.5 years of age

Bias in the SAK estimates of abundance will be directly related to the bias in $\hat{\theta}$. If the juvenile sex ratio is assumed too high, abundance estimates $\left(N_i \text{ and } N_{i+1}\right)$ will be positively biased. If the juvenile sex ratio is assumed too low N_i and N_{i+1} will be negatively biased.

8.4 Estimate of Fawn-to-Doe Ratio $\left(\hat{R}_{J/F}\right)$

Any bias in the fawn-to-doe ratio $\left(R_{J/F}\right)$ will have a direct effect on bias of the SAK abundance estimates $\left(\hat{N}_i \text{ and } \hat{N}_{i+1}\right)$. Overestimating the ratio will result in abundance being overestimated. Conversely, underestimating the fawn-to-doe ratio will result in an underestimate of total population abundance.

The fawn-to-doe ratio is predicated on equal detection rates for both fawns and does during visual surveys, which does not appear to be the case in July in Wisconsin (Robert Rolley, personal communication). Visual counts of fawns and does in early summer may underestimate recruitment because fawns are too young to travel with does (Downing et al. 1977, Roseberry and Woolf 1991, McCullough 1993, Rabe et al. 2002). Visual effects that result in an underestimate of fawns would downwardly bias the ratio $R_{J/F}$. Accurate estimates of $\hat{R}_{J/F}$ are also predicated on does without fawns being as detectable and reported at a similar rate as does with one or two offspring.

8.5 Estimate of Total Harvest $\left(\widehat{TH}_i\right)$

For abundance in year $i+1$ to be estimated without bias, an unbiased estimate of total harvest $\left(\widehat{TH}_i\right)$ in year i must be available. These estimates must include harvest numbers adjusted for noncompliance with reporting and wounding losses. Annual adjustments to the estimate of wounding loss may be needed to account for recovery rates that may depend on degree of snow cover, regulation type (Hardin and Roseberry 1975), etc. Noncompliance with reporting also may be high and variable (Rosenberry et al. 2004, Hansen et al., in press).

Any bias in the estimate of total harvest $\left(\widehat{TH}_i\right)$ will have an inverse effect on the bias of annual abundance estimates $\left(\hat{N}_{i+1}\right)$. Systematically underestimating total harvest in year i will produce an overestimate of deer abundance in year $i+1$. Conversely, overestimating total harvest in year i will produce an underestimate of deer abundance in year $i+1$.

8.6 Estimate of Lambda $\left(\hat{\lambda}_i\right)$

Any bias in $\hat{\lambda}_i$ will have a direct effect on the bias of abundance estimates in year $i+1$. Overestimating overwinter survival and recruitment will produce an overestimate of total abundance $\left(\hat{N}_{i+1}\right)$. Underestimating $\hat{\lambda}_i$ will produce an underestimate of abundance in year $i+1$. For the Northern Forest region, a regression model is used to estimate $\hat{\lambda}_i$ based on a winter severity index. For other parts of Wisconsin, no empirical model appears to exist to predict $\hat{\lambda}_i$

based on prevailing environmental conditions. For these other regions, the statistical behavior of the $\hat{\lambda}$ estimates is unknown.

8.7 Estimates of Yearling Proportions $\left(\hat{p}_{YM}\right.$ and $\left.\hat{p}_{YF}\right)$

Annual buck mortality and the adult sex ratios are based on annual estimates of the proportion of yearling (i.e., 1.5-year-old) males and females in their respective subpopulations. These estimates are obtained by aging a sample of the sport harvest each year. The use of $\hat{p}_{YM}$ and $\hat{p}_{YF}$ in the SAK model assumes 1.5-year-old deer can be correctly differentiated from 0.5 and 2.5+ year olds. Systematic aging errors would bias the estimates of p_{YM} and p_{YF} with subsequent impacts on the SAK estimates. Should too many animals be classified as 1.5-year-old bucks, p_{YM} will be positively biased and subsequent SAK estimates, negatively impacted. Typically, the first few age classes of white-tailed deer can be accurately determined by tooth eruption and wear (Jacobson and Renier 1989), so classification error should be inconsequential. Using harvested deer to estimate yearling proportions also assumes equal vulnerabilities to harvest which under some conditions may be violated (Roseberry and Klimstra 1974).

Less obvious and more important biases can be introduced by violations of the assumptions of a stable and stationary population. When a deer population has a stable and stationary population then $\hat{p}_{YM}$ is a first-order (i.e., first-term Taylor series) unbiased estimator of total buck mortality, i.e.,

$$E\left(\hat{p}_{YM}\right) = 1 - S_{NM} S_{HM},$$

where

S_{NM} = natural survival rate of males;

S_{HM} = probability of surviving harvest for males.

When the population has a stable age distribution, but changing annual abundance at a finite rate of λ, then

$$E\left(\hat{p}_{YM}\right) = 1 - \frac{S_{NM} \cdot S_{HM}}{\lambda}, \tag{12}$$

not $1 - S_{NM} \cdot S_{HM}$. Similarly, when a population is stable and stationary, the quotient p_{YM} / p_{YF} is a first-order unbiased estimate of the adult sex ratio, i.e.,

$$E\left(\frac{\hat{p}_{YM}}{\hat{p}_{YF}}\right) \doteq \frac{E\left(\hat{p}_{YM}\right)}{E\left(\hat{p}_{YF}\right)} = \frac{1 - S_{NM} \cdot S_{HM}}{1 - S_{NF} \cdot S_{HF}} = R_{F/M},$$

where

S_{NF} = natural survival rate of females;

S_{HF} = probability of surviving harvest for females.

In the case of a stable but nonstationary population $\left(\text{i.e., } \lambda > 1 \text{ or } \lambda < 1\right)$,

$$E\left(\frac{\hat{p}_{YM}}{\hat{p}_{YF}}\right) \doteq \frac{1 - \dfrac{S_{NM} \cdot S_{HM}}{\lambda}}{1 - \dfrac{S_{NF} \cdot S_{HF}}{\lambda}} \neq R_{F/M}. \tag{13}$$

However, when the demographic structure of a population is perturbed, the population will not possess a stable age distribution, and the adjustments in Eq. 13 are unlikely to apply (Yearsley et al. 2004, Koons et al. 2006).

The bias due to $\lambda \neq 1$ will therefore affect the SAK estimator in two different ways, biasing both the adult sex ratio and the estimate of total buck mortality. Simulation studies were used to investigate the effect of model violations on the resulting SAK estimates of N_i. The direction of bias in N_{i+1} will be the same as that observed for $\hat{N}_i$.

9.0 Deterministic Effects

Using a deterministic two-sex Leslie Matrix model (Appendix B), annual population abundance and harvest were calculated under both stable-stationary conditions and nonstable-nonstationary conditions. Under stable-stationary conditions, the SAK, as expected, tracked the modelled population abundance (Figure 1). However, when the population had a stable age-sex composition but population abundance was increasing annually (i.e., nonstationary, $\lambda > 1$), the SAK model underestimated N_i (Figure 1b). Conversely, when the population was decreasing at a constant rate of $\lambda < 1$, the SAK has a tendency to overestimate N_i (Figure 1c). The degree of bias will depend on the degree of departure from $\lambda = 1$ per Eqs. (12) and (13).

A modified SAK model for $\hat{N}_i$ under stable-nonstationary conditions can be written as

$$\hat{N}_i = \frac{H_i}{\left(1-\lambda\left(1-\hat{p}_{YM}\right)\right)\hat{B}}\left[1+\frac{\left(1-\lambda\left(1-\hat{p}_{YM}\right)\right)}{\left(1-\lambda\left(1-\hat{p}_{YF}\right)\right)}\theta+\frac{\left(1-\lambda\left(1-\hat{p}_{YM}\right)\right)}{\left(1-\lambda\left(1-\hat{p}_{YF}\right)\right)}\theta R_{J/F}\right]. \qquad (14)$$

Typically, if λ is near 1 (i.e., 0.95-1.05), the bias will be relatively small.

Alternatively, a sudden population or harvest shift can have an immediate and substantial impact on the SAK estimates. Figure 2 illustrates a population that went from a stable-stationary condition at $N = 50{,}000$ to a new state when the buck harvest mortality (M_H) went from 0.30 to 0.20 and back again. After each harvest regime shift, the SAK estimate asymptotically converged on the new stable-stationary condition. However, at the time of the shift, the SAK estimates expressed substantial bias. When the buck harvest mortality was increased, the SAK estimator underestimated actual abundance (i.e., negative bias). When buck harvest mortality was decreased, the SAK estimator overestimated actual abundance (Figure 2).

Consequently, sudden and severe shifts in hunting regulations or changes in hunting conditions can dramatically impact SAK estimates. Greater buck hunting pressure can falsely predict increased abundance and reduced buck hunting pressure can falsely predict decreased abundance immediately after the regulation changes (Figure 2). These biases are not substantially diminished going from annual estimates of $\hat{p}_{YM}$ and $\hat{p}_{YF}$ (Figure 2a) to moving averages (Figure 2b).

A similar shift in the doe harvest rate from 0.05 to 0.15 (Figure 3) did not produce the same shift in abundance estimates as the buck harvest changes. The SAK estimates followed abundance trends quite well, with a slight positive bias as seen in Figure 1a.

10.0 Stochastic Effects

Deer recruitment and survival can be directly affected by annual changes in overwinter conditions and long-term habitat changes. Recruitment and survival also are affected by processes of random chance. For example, you would not expect to always see 5 heads and 5 tails in 10 flips of a fair coin. Random chance will cause the outcomes to deviate from the long-run expectation of 50:50. However, the more flips of the coin, the closer the overall outcome will be to that 50:50 expectation. The same is true in wild populations; small populations are subject to relatively more random fate than large populations, but all populations experience it. To understand the effects random fluctuations in survival or recruitment might have on the SAK estimates, a stochastic, two-sex Leslie matrix model was constructed (Appendix B). Natural survival and harvest were modeled as binomial processes while annual recruitment was modeled as a Poisson process. We examined the effect of random demographic changes in age and sex composition on the SAK abundance estimator $\left(N_i\right)$.

The stochastic survival and recruitment processes caused the simulated deer populations to fluctuate about their equilibrium abundance (Figure 4). However, random fluctuations in age composition used in estimating p_{YM} and p_{YF} resulted in the SAK abundance estimates of N_i to vary much more widely than the populations they were monitoring. In a population of approximately 50,000 deer, the coefficient of variation $\left(\mathrm{CV} = \left(s/\overline{x}\right) \times 100\%\right)$ was 4.6%. As expected, as the population size decreased, the amount of random demographic process error in the SAK estimate increased. For a population of 25,000 deer, the CV was 8.3%, whereas for 10,000 deer, the CV was 12.4%. For a DMU with 10,000 deer, this translates into the ability to estimate abundance within $\pm 24.3\%$ of the true value, 95% of the time. Hence, random fluctuation in recruitment and/or survival will cause the SAK estimate to vary, but the effect dampens as the size of the surveyed population increases. This is one reason why the SAK estimates may be reasonably precise at the state level, but not at the deer management unit (DMU) level. We also assessed whether using running averages of p_{YM} and p_{YF} helped dampen the random demographic error (Figure 5). The averages helped dampen the variability, but not by much (Figure 5).

Because covariance among vital rates is an important contributor to population fluctuation in deer populations (Coulson et al. 2005), we performed additional simulations incorporating covariance between survival and productivity (Figure 4). To induce a positive covariance between survival and productivity, compound processes were used in generating the age class data. Under the compound process, survival to the next age class was simulated as

$$n_{i+1} \sim \mathrm{Bin}\left(n_i - c_i, S_i\left(1+\varepsilon_k\right)\right)$$

and productive of juveniles as Poisson with parameter

$$E\left(n_0\right) = \sum_{j=0}^{A}\left(n_i - c_i\right)F_i\left(1+\varepsilon_k\right)$$

where ε_k is uniformly distributed $U\left(-0.20, +0.20\right)$ in year *k*.

Each year, we used a new randomly generated ε_k which either increased or decreased survival and productivity by ε_k 100% in expectation. For example, if $\varepsilon_k = 0.05$, both the parameters F_i and S_i increased by 5% over baseline conditions that year. An $\varepsilon_k = -0.05$ would result in F_i and S_i being decreased to 95% of their typical value. Other distributions and ranges for ε_k could be used, but this is adequate for demonstration purposes.

We compared the error in estimation, i.e.,

$$\mathrm{SE}\left(\widehat{\mathrm{SAK}}\right) = \sqrt{\widehat{\mathrm{Var}}\left(\widehat{\mathrm{SAK}}\right)} = \sqrt{\frac{\sum_{k=1}^{n}\left(\hat{N}_{\mathrm{SAK},k} - N_k\right)^2}{n}}$$

where n = 1000 years of data simulated under two scenarios:

1. No correlation, i.e., $\varepsilon_k = 0$.
2. Positive correlation, i.e., $\varepsilon_k \sim U\left(-0.20, +0.20\right)$.

Observed values for the standard error of estimation in the SAK model under different degrees of correlation between survival and fecundity were as follows:

Distribution of ε	$\mathrm{SE}\left(\widehat{\mathrm{SAK}}\right)$
No correlation, $\varepsilon = 0$	1327.2
Positive correlation, $\varepsilon_j \sim U\left(-2, +2\right)$	1818.6

With a positive correlation between survival and productivity, both the variability in the simulated abundance and the error in estimation of the SAK model increased. Any demographic process that cause the population to deviate from the assumptions of a stable age distribution and stationary abundance will violate the SAK abundance estimator. Both the estimate of annual male mortality (Burgoyne 1981, Heincke 1913) and the estimate of the adult sex ratio

(Severinghaus and Maguire 1955) are based on these two conditions. Adding correlation between productivity and survival only exacerbates the situation, making the SAK model behave worse.

Last, we also performed simulations to determine how large a deer population had to be before the stochastic elements of demographics had an insignificant effect on the SAK estimate (Figure 6). These results indicate that population sizes need to be 1–2 million before this demographic noise is trivial, drawing into question SAK estimates at a single DMU scale. Upon this noise we need to add the sampling error discussed below in section 11.0.

11.0 Sources of Sampling Error

11.1 Sampling Precision of Abundance Estimate, N_i

In section 10.0, inputs to the SAK estimators were exact demographic values measured from a complete tally of the population and its constituents. Values of fawn:doe rates $\left(R_{J/F}\right)$ and buck recovery rate (*B*) were treated as known constants without error. Our simulations examined estimation bias (or systematic error) under ideal conditions of no sampling error.

However, there is a second source of error associated with subsampling the population and harvest to estimate p_{YM}, p_{YF}, and $R_{J/F}$. This uncertainty adds random error to the input parameters and, consequently, to the abundance estimates. Any estimate of a population parameter (e.g., proportion of yearlings in the population) that is based on a subsample of the population is subject to random variation. That is, the resulting estimate could differ from sample to sample even if the population itself did not change. The precision, or repeatability, of an estimate is dependent on sample size. Large samples will be more precise because they use more information to estimate the characteristic of the population being measured. For example, a fair coin is equally likely to land heads or tails, but if this coin is tossed only two times it could conceivably result in anywhere from 0 (0%) to 2 (100%) heads. Based on only two tosses it is very difficult to assess whether it is truly a fair coin. However, if we toss this coin 100 times it is highly unlikely to result in zero (or 100) heads; rather the percentage of heads is likely to be very close to 50% if it is truly a fair coin – and a second 100 tosses should provide a similar result.

The precision of population estimates for Wisconsin's SAK model are dependent on the amount of data collected to estimate the various input parameters. Hence, statewide population estimates will always be more precise than Deer Management Unit (DMU) estimates because more data are available (e.g., more harvested deer aged, more fawn and doe sightings, etc.) at the statewide level. However, before one can judge whether the precision of a population estimate is acceptable, some criterion for an acceptable estimate must be chosen. Robson and Regier (1964) identified three levels of precision for abundance studies. At the least precise level is a population estimate that is within 50% of the true population estimate 95% of the time, which they considered useful only for management surveys where a rough idea of population size is needed. At the other extreme, population estimates within 10% of the true population size 95% of the time are recommended for careful research into population dynamics. Robson and Regier (1964) suggested that population estimates within 25% of the true population size 95% of the time were sufficient for accurate population management.

The precision of an estimator can be measured in different ways. This section will primarily rely on the coefficient of variation (CV), which is the ratio of the standard error divided by the estimate (times 100%). The standard error is a measure of the variability about the point estimate; thus, the CV is simply the size of the standard error relative to the point estimate. For example, if a coin is tossed 10 times and 5 heads result, the following statistics can be calculated:

No. heads = 5, standard error = 1.58, CV = 1.58/5 = 31.6%.

However, if we toss this same coin 100 times and obtain 50 heads we obtain the following:

No. heads = 50, standard error = 5, CV = 5/50 = 10.0%.

Thus, the precision of the estimate of the number of heads for 100 tosses is much more precise (CV = 10%) than for the same coin for only 10 tosses (CV = 31.6%). The number of heads and the standard errors are not comparable because they are based on a different number of tosses, but the standard errors relative to their respective means (CV) are directly comparable and the CV is much smaller for the estimate based on 100 tosses.

If we use Robson and Regier's (1964) benchmark of population estimates being within ±25% of the true population size 95% of the time to be useful for accurate management decisions, then the CV of population estimates must be approximately $\leq$12.5%. A CV = 25% would be equivalent to the least precision level (±50% of the true population size 95% of the time) and a CV = 5% would be acceptable for careful research into population dynamics (±10% of the true population size 95% of the time).

Another measure of precision of a population estimate is the confidence interval. The confidence interval is a statistical measure of the precision of a population estimate that is commonly misinterpreted. If we assume an underlying distribution of the estimator and have an estimate of population size and standard error, we can calculate a confidence interval with a specified level of confidence that this interval will encompass the true population value $(1-\alpha)$100% of the time. This confidence interval should not be interpreted as upper and lower bounds on the true population size. In this report, 90% confidence intervals (90% CI) are calculated.

The guidelines provided by Robson and Regier (1964), although based on rigorous statistical methods, are predicated on *ad hoc* criteria of what level of precision provides useful population estimates for different research and management purposes. Thus, it should not be assumed that a population estimate that is found to be within 30% of the true population estimate 95% of the time is useless for management purposes. Instead, these guidelines should simply serve as useful benchmarks for comparison to the population estimates and associated measures of precision (CV and 90% CI) for DMUs using Wisconsin's SAK model. The objectives of section 11.0 are as follows:

1. Estimate the precision of population estimates for DMUs by calculating the CV and 90% confidence limits for a select number of DMUs during the years 1990–2005.
2. Evaluate which inputs to the SAK model contribute the greatest amount of variability to DMU population estimates.
3. Evaluate the precision of DMU population estimates if samples sizes used to estimate input parameters were increased and stabilized.

Data collected by WI DNR personnel for input into the SAK model were provided by Robert E. Rolley (WDNR) for the years 1986-2005 (except DMU 49B; 1990-2005). These data were for 16 selected DMUs that were deemed representative of the range of environmental and management scenarios that occur in Wisconsin (Figure 7, Table 1). The dataset included, by year and DMU, the number of deer harvested and the age-sex structure for antlered and antlerless harvests and the number of sightings of adult females and fawns during summer sighting surveys.

Additional information, although not DMU or year specific, provided data for other input parameters in the SAK model. Embryos of adult females inspected during 1982–87 (McCaffery et al. 1998) provided data to estimate fetal sex ratios. A nonlinear equation that described the relationship between the proportion of yearling males in the harvest and the buck recovery rate also was provided, although the coefficients in this equation had no measure of statistical precision.

No data were available for the proportion of the harvest not reported and the proportion of the harvest not recovered by hunters. Instead, Wisconsin DNR assumes 15% of the harvest each year is either shot and not recovered or not reported. This parameter value is based on some empirical data (e.g., Kubisiak et al. 2001), but no measure of statistical precision is available.

We used a Monte Carlo approach to estimate precision of Wisconsin SAK population estimates for two reasons. First, not all parameters in the model had associated measures of precision (i.e., variance estimates) hence the generic variance expressions derived by Skalski and Millspaugh (2002) could not be used. Second, the Wisconsin SAK model for some input parameters combines data across years (i.e., calculated parameters using 5-year running averages) to increase sample size and minimize temporal variability, which complicates the derivation of variance expressions. A Monte Carlo approach also has advantages over a Taylor series approximation approach (Seber 1982:7-9) because it makes no assumptions about the asymptotic properties of the estimators.

A Monte Carlo approach to estimating precision of a parameter assumes an underlying distribution for each variable in the model with a specific mean and variance. As an example, the abundance of the antlered deer population (N_A) could be estimated by dividing the number of bucks killed (H) by the harvest rate (h) of the buck population. If the harvest rate (h) of antlered deer were assumed to follow a binomial distribution, with $h = 0.65$ based on monitoring the fate of 200 radiocollared antlered deer ($Var(R) = h(1-h)/n$ = 0.00114) during the hunting season, the distribution of this harvest rate estimate would look like Figure 8.

For this simple example, $\hat{N}_A = H / \hat{h}$ and the variance could be easily derived using the same methods as used by Skalski and Millspaugh (2002). However, a Monte Carlo approach to estimating the variance of the population estimate simply would involve generating, say, 999 random variates for h (having the same mean and variance) and dividing each of the random variates into H to obtain 999 estimates of N_A. The standard deviation (SD) of these 999 estimates of N_A would be the measure of the standard error (SE) of $\hat{N}_A$. This same approach was used to evaluate the precision of the SAK model, which is much more complicated because it contains multiple input variables.

In addition to the assumption that the proportion of the harvest not recovered by hunters was constant and without error, we made the following assumptions about the distribution of input variables in the model:

H_A and H_{AL}	Antlered (H_A) and antlerless (H_{AL}) harvest were assumed to be known without error.
p_{YM} and p_{YF}	The proportion of yearling males (p_{YM}) and females (p_{YF}) in the population were assumed to be distributed binomially (B[n,p]) with mean $p = p_{YM}$ or p_{YF} and n = number of deer aged for the appropriate age-sex class and year.

$\hat{B}$ The buck recovery rate was calculated using equation (Eq. 5) and each parameter in this equation was assumed to be distributed normally with a standard error based on an assumed CV = 0.05.

$\hat{R}_{F/M}$ The proportion of female embryos was assumed to be constant and binomially distributed based on data obtained during 1982-87 (McCaffery et al. 1998).

$\hat{R}_{J/F}$ The proportion of fawns sighted during summer sighting surveys was assumed to be binomially distributed

These analyses assumed that parameter estimates were unbiased and that the population was stationary and had a stable age distribution; thus, the results simply evaluate precision of population estimates and do not address stochastic variability or demographic model violations (i.e., the stable and stationary population assumptions) issues related to bias in population estimates. The calculations were conducted using code programmed in SAS (SAS Institute, Cary, North Carolina, USA; Appendix C) and the built-in functions in SAS that generate random normal and binomial variates (see Appendix C). For each year and DMU, 999 replicate population estimates were calculated in which parameter estimates varied according to their assigned underlying distribution. These replicate population estimates were used to estimate a CV (= SD/$\bar{x}$ × 100%) and the 5^{th} and 95^{th} percentiles were used to construct 90% confidence intervals.

The population estimates from these simulations will differ from published estimates from Wisconsin DNR for several reasons. First, in the simulations no *ad hoc* adjustments were made to any input parameters, such as the buck recovery rate or fawn:doe ratio. Second, the values for $\hat{p}_{YM}$, $\hat{p}_{YF}$, and $\hat{R}_{J/F}$ were always calculated as 5-year running averages weighted by sample size (see Eq. 9). Third, changes in regulations (e.g., changes in the boundaries of DMUs) resulted in changes in harvest counts that differed from official DNR results, which we did not attempt to adjust in the simulations. Fourth, data from surrounding units were not combined. Consequently, it is important to recognize that the estimates of precision in this report should be used simply as an assessment of the precision of Wisconsin's population estimates rather than as a statistically rigorous evaluation. This is because several input parameters lacked associated variance estimates, and their contribution to the variability in population estimates either were ignored (e.g., wounding loss and unreported harvest rate) or estimated (e.g., buck recovery rate).

To evaluate which input variables contributed the greatest amount of variability to population estimates, we calculated mean CVs (averaged over years) for population estimates by DMU in which only one input variable at a time was allowed to vary. The proportion of each variable to the sum of CVs from all variables was used as a measure of the relative contribution of each variable to overall variability in population estimates. If this analysis identified one or several variables that consistently contributed the greatest amount of variability to population estimates then changes in the allocation of sampling effort among input variables could potentially result in more precise population estimates.

Also, we evaluated the effect of increasing the sample size of the number of antlered deer aged each year, the number of antlerless deer aged each year, and the number of deer sighted during summer sighting surveys to estimate fawn:doe ratios. We retained the same age structure and fawn:doe ratios in the simulations but increased the number of deer aged to 600/ DMU/year and the number of sightings of fawns and does to 100, 200, and 400 deer/DMU/year.

The CV for most DMUs and years ranged from 11 – 23% and the average CV ≈ 15% for all DMUs (Table 2). Relative to the benchmarks defined by Robson and Regier (1964), these results fall in the lowest to intermediate categories of precision with population estimates being within 25–50% of the true population size 95% of the time. Graphs of estimated population size and 90% CIs, by DMU and year, are presented in Figures 9-16.

The results of investigating which input variables contributed the greatest amount of variability to the population estimates indicated no one variable was consistently the greatest contributor to the overall variability of population estimates (Figure 17). Across the DMUs examined, the contribution of input variables to overall CV was variable. This is probably to be expected because sample sizes of number of harvested deer examined, number of summer sightings of deer, etc. all varied greatly over time and across DMUs (see Table 1).

Population estimates in which input values for the age structure of the antlered and antlerless harvest were not changed but the sample size (no. deer aged from the antlered harvest) was increased to 600 bucks per DMU per year resulted in little change in the precision of population estimates (Table 3 compared to Table 2). However, increasing and stabilizing the number of deer aged from the antlerless harvest did decrease the CV of population estimates by 1–3 percentage points for most units and greatly reduced the variability in the precision of population estimates (compare Table 3 to Table 2). Increasing and stabilizing the number of deer sighted during summer sighting surveys had little effect on the precision of population estimates (compare Table 4 to Table 2).

The results of this analysis suggest that the precision of population estimates, when ignoring stochastic variability inherent in demographic processes, given the data collected by Wisconsin DNR and as calculated using the Wisconsin SAK model, are good to fair as compared to the benchmarks defined by Robson and Regier (1964). Most CVs in this analysis were <20% and the average CV was approximately 15%. This means that these population estimates are within 30–40% of the true population size 95% of the time, assuming all assumptions were met and input parameter estimates were unbiased.

However, there are several important caveats to this interpretation of the results. First, two input variables are assumed to have no error (antlered and antlerless harvest) and two others have no estimate of precision (buck reporting rate and wounding loss and unreported harvest rate). Second, these results are for selected units in which relatively large sample sizes exist for the three input parameters collected on an annual basis (fawn:doe ratio, proportion of yearling bucks, and proportion of yearling does). Smaller units with limited sample size will exhibit poorer precision. Third, the parameters used to estimate the buck reporting rate were assumed to have a CV = 5%. If the CVs for coefficients in the formula used to calculate the buck reporting rate were on the order of 10%, the average CV for population estimates would be >20% for all DMUs. Fourth, simulations equal stochastic variability in observed values of p_{YM} and p_{YF} which was shown to be important in populations less than 10,000 (see Section 10.0). The sampling error must be added to stochastic variability of demographic processes to describe total variability, which is done in Section 11.3.

One useful analysis of the precision of population estimates is to evaluate which component(s) of the model contribute the most to the variance of population estimates. Both the results of the contribution of individual input values to the CV (Figure 17) and the results of increasing and stabilizing sample sizes (Tables 3 and 4) indicated that variability in sample sizes over time had the greatest influence on the precision of population estimates (see Table 1), which has been recognized by WI DNR (WDNR 2001). Increasing the number of sightings of adult females and fawns during the summer sighting surveys from 100 to 400 deer per DMU per year resulted in little overall improvement in the precision of population estimates. However, these analyses did suggest that greater consistency in the number of deer aged from the antlerless harvest could result in noticeable improvement in the precision of population estimates (see Table 3 compared to Table 2).

From this precision work, we conclude the following:

1. Two input parameters (buck recovery rate and the wounding loss and unreported harvest rate) have no associated estimate of precision. This means that a statistically rigorous analysis of the precision of Wisconsin's deer population estimates is impossible.
2. If the coefficients in the equation used to estimate the buck reporting rate are assumed to have CVs of 5% then Wisconsin's deer population estimates have CVs of approximately 15% in the DMUs with the most robust data. If the buck reporting rate equation is composed of coefficients with CVs of 10% then population estimates will have CVs >20% not considering stochastic variability.
3. This level of precision means that DMU population estimates are within 30–40% of the true population size 95% of the time, assuming that population estimates are unbiased, and there is no stochastic variability (section 11.3 considers stochastic variability of demographic processes that should be considered). Robson and Regier (1964) recommended that population estimates for management purposes should be within 25% of the true population size 95% of the time.

4. No one input variable was consistently associated with contributing the greatest amount of variability to population estimates. Skalski and Millspaugh (2002) reported similar conclusions based on their evaluation of a generic variance expression for the SAK model.
5. More consistency in the number of deer aged (over time) from the antlerless harvest would likely have the greatest benefit in reducing the variability in precision of population estimates.

11.2 Precision of λ and Its Effect on the Precision of $\hat{N}_{iH}$

The major component associated with the projection of deer abundance from year i (i.e., $\hat{N}_i$) to year $i+1$ (i.e., $\hat{N}_{i+1}$) is the value of the posthunt-prehunt λ. This λ is a multiplier that expresses the relative change in abundance immediately posthunt to the prehunt abundance the next year. It is an expression of anticipated overwinter survival and fawn recruitment. In the Northern Forest region an analytical model establishes this important multiplier. A model is not available for other regions of the state; thus model precision cannot be assessed.

In the Northern Forest region, a linear regression model predicts λ based on a winter severity index. The fitted regression model has an $r^2 = 0.4717$ ($r = -0.6868$ [sic]) with an MSE of 0.02579. The variance for predicting a new value of λ from a new value of the winter severity index is

$$\mathrm{Var}\left(\hat{\lambda}\right) = \mathrm{MSE}\left(1 + \frac{1}{n} + \frac{\left(x_i - \bar{x}\right)^2}{\sum\left(x_i - \bar{x}\right)^2}\right),$$

which has the expected value of

$$\mathrm{Var}\left(\hat{\lambda}\right) = \mathrm{MSE}\left(1 + \frac{2}{n}\right)$$

over all values of the independent variable (x_i). In the case of the Northern Forest region, this is equivalent to

$$\widehat{\mathrm{Var}}(\hat{\lambda}) = 0.02579\left(1+\frac{2}{32}\right) = 0.02740$$

or a CV of 0.13577 $\left[\widehat{\mathrm{SE}}(\hat{\lambda})/\bar{\lambda}\right]$. This implies that the regression model will produce an estimate of λ within $\pm 26.6\%$ of the true value, 95% of the time. This level of uncertainty is added to the uncertainty in the estimate of $\hat{N}_i$ when projecting $\hat{N}_{i+1}$.

More specifically, the variance of $\hat{N}_{i+1}$ can be approximated by the delta method to be

$$\begin{aligned}\mathrm{Var}\left(\hat{N}_{i+1}\right) &= \mathrm{Var}\left(\left(\hat{N}_i - \widehat{TH}_i\right)\hat{\lambda}_i\right)\\ &= N_{i+1}^2\left[\mathrm{CV}\left(\hat{N}_i - \widehat{TH}_i\right)^2 + \mathrm{CV}\left(\hat{\lambda}\right)^2\right].\end{aligned} \tag{15}$$

In turn, the CV for $\hat{N}_{i+1}$ can be expressed from Eq. (15) as

$$\mathrm{CV}\left(\hat{N}_{i+1}\right) = \mathrm{CV}\left(\hat{N}_i - \widehat{TH}_i\right)\sqrt{1+\frac{\mathrm{CV}\left(\hat{\lambda}\right)^2}{\mathrm{CV}\left(\hat{N}_i - \widehat{TH}_i\right)^2}}\,. \tag{16}$$

In Eq. (16), $\hat{N}_i - \widehat{TH}_i$ is the immediate postharvest deer abundance in year i. The CV for $\hat{N}_{i+1}$ is equivalent to that of $\hat{N}_i - \widehat{TH}_i$ times the second term in Eq. (16).

A couple of examples may help illustrate the consequences of Eq. (16) and the effect of imprecision in $\hat{\lambda}$ on the overall precision of the prehunt abundance $\hat{N}_{i+1}$. Assume the immediate posthunt precision is $\pm 20\%$, 95% of the time (i.e., ε = 0.20), implying a CV $\left(\hat{N}_i - \widehat{TH}_i\right)$ = 0.10204. Then, Eq. (16) suggests the CV of $\hat{N}_{i+1}$ will be

$$\mathrm{CV}\left(\hat{N}_{i+1}\right) = 0.10204\sqrt{1+\frac{(0.13577)^2}{(0.10204)^2}} = 0.1024(1.663) = 0.1697\,.$$

The error in estimation from $N_i - TH_i$ to N_{i+1} increased by 66.3% because of the additional uncertainty in $\hat{\lambda}$. The prehunt abundance estimate N_{i+1} now has a precision of $\pm 33.3\%$ of the true value, 95% of the time.

11.3 Total Variability, Stochastic and Sampling Error

We performed additional stochastic simulations incorporating sampling error as well as demographic process variability (Section 10.0, Figure 6) to examine the overall precision of the SAK estimates at the DMU level. We started with a stable-stationary population of 10,000 deer (Figure 18a). To that population, we added binomial error to the survival and harvest processes and Poisson error to recruitment (Figure 18b) consistent with the methods of Section 10.0. Next, we added binomial sampling error in the estimate of p_{YM}, p_{YF}, and $R_{J/F}$. For age composition, we randomly sampled 250 1.5+ year old bucks and 250 1.5+ year old adult females in the harvest. These samples are consistent with the approximately 5% sampling rate used in Wisconsin (Robert Rolley, personal communication). In estimating $R_{J/F}$, we randomly sampled 160 individuals, again consistent with typical sampling rates used by WDNR, of 80 does and a 1:1 ratio (WDNR 2001:6.1). The demographic stochasticity alone produced a CV of 12.1%. Adding sampling error to these demographic values increased the overall CV to 58.4% (Figure 18c). Finally, we generated estimates of the buck recovery rate (*B*) with a CV of 10%. This additional source of uncertainty raised the overall CV to 62.2% (Figure 18d). In other words, with both demographic stochasticity and sampling error at DMU levels of effort, the resultant abundance estimates, $\hat{N}_i$, were within $\pm 121.9\%$ of the simulated population level, 95% of the time.

Results from these studies suggest that SAK estimates for DMUs are inherently imprecise. Given *perfect sampling* (i.e., Figure 18b), precision would be $\pm 23 - 24\%$ of the true abundance, 95% of the time; however, we must also consider stochastic variability of demographic processes. The only practical solution is to monitor deer abundance at larger geographic scales where stochastic variation is relatively reduced and sample sizes for estimating p_{YM}, p_{YF}, and $R_{J/F}$ are increased.

12.0 Evaluations of the Accuracy of SAK Population Estimates

The bias associated with SAK population estimates can be measured only if the true population size is known without error. For a DMU it is not feasible to know true population size, although it has been accomplished for small areas (e.g., Kubisiak et al. 2001). Deer biologists in Wisconsin have recognized this fact and have tried to collect circumstantial evidence to evaluate the bias associated with SAK population estimates, or at least obtain information to indicate whether SAK population estimates are reasonable given other information known about the deer population (see WDNR 2001, Chapter 6, pp. 38-44).

One approach to evaluating the SAK model is to see how strongly it is correlated with other population indices (e.g., road-killed deer counts). An indicator of how strongly correlated two variables are with each other is the Pearson product-moment correlation coefficient (r). The value of r can range from 0 (no correlation) to 1 (perfect correlation).

In Wisconsin, SAK population estimates have been correlated with deer-trail surveys (r = 0.94; McCaffery 1976). Also, counts of vehicle-killed deer indicated strong correlations with buck harvests ($r > 0.78$ except for Area XIII; McCaffery 1973), as well as SAK population estimates ($r > 0.56$ except in the Central Forest region; WDNR 2001). Finally, helicopter surveys of DMUs have correlated with SAK population estimates ($r = 0.91$; WDNR 2001) and the relationship between the actual deer harvest and that predicted by SAK have been presented as support for the accuracy of the SAK model (r = 0.89–0.98; WDNR 2001).

In light of this circumstantial evidence that suggests that the SAK model is a good estimator of deer abundance, it seems incongruous that the evaluation of the assumptions of the SAK model (Section 7 and 8) and the precision of population estimates (Section 9 and 11) outline substantial concerns with this approach to modeling deer populations. However, we believe some of the correlations presented as evidence in support of the SAK model are not the most appropriate methods of assessing model performance.

In particular, the correlations between SAK-predicted and actual buck harvests (Figure 6.27 in WDNR 2001) imply that the SAK model accurately predicts future harvests. However, the strong correlation coefficients ($r \geq 0.81$; Table 5) occur because DMUs with large deer populations are likely to have large actual and predicted harvests in subsequent years, and DMUs with small populations are expected to have small actual and predicted harvests. In fact, a stronger correlation can be obtained by simply using last year's buck harvest to predict the current years' buck harvest. Using predicted and actual harvests for 16 selected DMUs, we found in 12 of 14 years the previous year's harvest correlated more strongly with actual harvest than the predicted harvest (Table 5). Therefore, the strong within-year correlations between SAK-predicted and observed buck harvests do not provide strong support for the performance of the SAK model.

A more appropriate evaluation of the SAK model is the correlation between predicted and observed harvests *for a single DMU over time*. This distinction is important because management decisions occur at the DMU level and only the performance of the model within a given DMU over time is relevant. Table 6 presents the correlation between actual harvest and the predicted and previous years' harvest. In all but 2 DMUs, the predicted harvest is more strongly correlated with actual harvest. Although overall the correlation is weaker ($\bar{r} = 0.62$, range =

0.08–0.84), it is evident that the SAK model yields estimates of deer population size that allow better predictions of future harvests than simply relying on past harvests to predict future harvests ($\bar{r} = 0.45$).

We believe the most appropriate evidence for evaluating the performance of the SAK model would be correlations of population predictions with other population indices over time *within a single DMU*. Unfortunately the evidence presented in the *Management Workbook for White-tailed Deer* (WDNR 2001) showing that deer-trail counts, pellet counts, and helicopter surveys are strongly correlated with SAK population estimates, and that predicted vs. actual harvest are strongly correlated, constitute weak or misleading circumstantial evidence in support of the SAK model. This is because these correlations are among DMUs, not for a given DMU over time. We note, however, that the among-year correlation between road-kill counts and SAK population estimates is appropriate, although the analysis pooled data across multiple DMUs and thus is not at the same scale at which deer management decisions are made.

In conclusion, the SAK model seems to be incorporating biological information such that wildlife managers, for most DMUs, are able to make reasonable predictions of upcoming harvests. However, for the 16 DMUs evaluated, the SAK model can account for only up to an average of 62% of the variability in annual deer harvests, as opposed to the 64–94% suggested by the graphs presented in WDNR (2001). What appeared to be strong support for the SAK model predictions presented by WDNR (2001) was an inappropriate and misleading evaluation of the predicted and actual harvest data. In some DMUs we note that the predictive capability of the model is especially poor (e.g., DMU 28; Table 6), which may occur because of violations of model assumptions (Section 7 and 8) and the inherent variability associated with sampling small populations and stochastic variability (Section 9.1).

13.0 A Review of Alternative Population Estimation Methods

Many different approaches to estimating animal abundance have been developed and the statistical foundations of these techniques are described in detail by Seber (1982), Williams et al. (2003), and Skalski et al. (2005). However, some techniques are not well suited to estimating abundance of white-tailed deer. Skalski et al. (2005) described methods and assumptions of techniques applicable to big game species and Roseberry and Woolf (1991) provided a critical evaluation of models commonly used to estimate abundance of white-tailed deer.

In this section, we provide a brief review of selected abundance estimation alternatives to the Wisconsin SAK model, how they may be applicable to Wisconsin, and important advantages and challenges of applying each technique (see Table 7). We direct the reader to Skalski et al. (2005) for a detailed description of the applications for each abundance estimation method. Finally, we provide a summary of how other state wildlife agencies monitor their white-tailed deer populations and compare those methods to the Wisconsin SAK model.

13.1 Index methods

An index is some measure of a population characteristic that does not provide a direct estimate of abundance but can be used to monitor changes in population abundance over time. For example, McCaffery (1976) used deer-trail counts to monitor deer abundance over time and relative abundance among DMUs. Advantages of index methods are that they are usually relatively simple and inexpensive to implement. The disadvantage is that few indices have been validated to actually correlate with true abundance. Consequently, the assumption that changes in the index reflect changes in population size is tenuous. For this reason, Skalski et al. (2005:433) noted that "index studies may be adequate for developing working hypotheses or monitoring general trends but insufficient for consummate investigations of critical resource issues." We do not recommend the use of indices as an alternative to other population monitoring methods.

13.2 Distance sampling

The statistical theory behind distance sampling methods has been well developed (Buckland et al. 2001, 2004). The basic idea is that if survey transects are placed randomly across a study area, the number of detected objects for a given perpendicular distance will decline in some fashion with increasing distance from the transect line. An important assumption, however, is that all objects on the transect line are detected. By modeling the distribution of distances deer are detected from the transect line (i.e., modeling the detection function), one can estimate the proportion of deer observed and, thus, obtain a population estimate with measures of statistical precision.

The advantage of this technique is that deer do not have to be captured and marked (e.g., radiocollared) and the modeling of the detection function can incorporate differences in detection due to observer or environmental conditions. The disadvantage is that transects cannot be readily placed randomly across the study area and typically investigators use roads as the sampling transects (e.g., Underwood et al. 1998). Consequently, resulting population estimates are likely biased because transects are not distributed randomly with respect to the distribution of deer. Furthermore, dense vegetation may make detection of deer difficult and adult males are less likely to be seen than antlerless deer. Finally, surveys conducted in winter may not be able to distinguish between adult male and female deer.

Distance sampling methods have been used on small areas, such as national parks, where random transects can be placed on the landscape (M. Sturm, Assateague Island National Seashore, personal communication). However, deployment at the scale of a DMU has not been attempted and would be very labor intensive. Consequently, distance sampling methods are unlikely to be practical as a population monitoring tool for state wildlife agencies.

13.3 Aerial Surveys and Sightability Models

Pollock and Kendall (1987) reviewed a variety of statistical models for estimating animal abundance via aerial surveys. However, most of these methods rely on marked animals (e.g., radio-collared deer). Samuel et al. (1987) and Steinhorst and Samuel (1989) developed the techniques and statistical formulation for estimating the proportion of animals detected during aerial surveys. In this technique marked animals are used to develop a model to predict detection probability that is applied to operational surveys when no marked animals are available. The technique involves radio-collaring animals and then conducting aerial surveys to estimate the proportion of collared animals detected. This information is used to build a sightability model which estimates the probability a given animal is detected. Detectability may be affected by animal behavior (running, standing, etc.), visual obstruction by vegetation, weather conditions (snow cover, cloud cover, etc.), and number of animals in a group.

This technique has been applied more often in the western U.S. on large ungulates, such as elk (*Cervus elaphus*; McCorquodale 2001) and moose (*Alces alces*; Anderson and Lindzey 1996). However, it has been applied to mule deer (e.g., Freddy et al. 2004), and white-tailed deer (Beringer et al. 1998) and elk in the eastern U.S. (Otten et al. 1993, Cogan and Diefenbach 1998). The critical assumption of this technique is that the sightability model developed with collared animals is applicable to future surveys of uncollared animals and often in different habitats. The technique is unlikely to perform well in areas with dense vegetation, especially conifer cover, because detection probabilities are extremely low, or essentially zero, and resulting population estimates will be biased and imprecise. Furthermore, Cogan and

Diefenbach (1998) found that undercounting when animals are in groups was likely to occur and result in negatively biased population estimates.

Aerial surveys are an expensive survey method. The Pennsylvania Game Commission (PGC) expended >$100,000 developing a sightability model for elk and approximately $40,000 per year (PGC, unpublished data) for an area equivalent to a typical Wisconsin DMU. Because of the expense, and unpredictable nature of snow cover, the PGC no longer uses this method to monitor elk abundance (J. DeBerti, PGC, personal communication). The Idaho Department of Fish and Game spends $500,000 in helicopter time for elk aerial surveys each year (P. Zager, personal communication). Also, aerial surveys are dangerous because of the low-altitude flying (c.f. Freddy et al. 2004) and aircraft crashes are the single greatest cause of occupation-related deaths for wildlife biologists (see http://www.aztws.org/Memorial_Garden.htm).

13.4 Change-in-Ratio Methods

The application of change-in-ratio methods is potentially useful when a differential harvest of animals occurs (e.g., the number of antlered deer harvested is greater than the number of antlerless deer relative to the ratio of antlered:antlerless in the population). Thus, a pre-harvest survey (e.g., a spotlight survey) would provide an estimate of the ratio of antlered:antlerless deer, followed by a hunt where antlered deer are harvested, followed by a post-harvest survey to obtain an estimate of the resulting ratio of antlered:antlerless deer. Pre- and post-harvest surveys of antlered:antlerless ratios and the number of antlered deer harvested can be used to estimate population size.

If both types of animals (e.g., antlered and antlerless deer) are harvested, then it is assumed that both antlered and antlerless deer have equal probability of being sighted during the pre- and post-harvest surveys. Roseberry and Woolf (1991) were critical of this technique for estimating white-tailed deer abundance because this assumption was violated and Skalski et al. (2005) noted that the estimator is not robust to this assumption violation. Paulik and Robson (1969) noted that the magnitude of the change in the ratio of antlered:antlerless deer from pre- and post-hunt surveys must be >0.05 and preferably >0.10 because estimates lack precision if little change in the ratio occurs. Finally, Williams et al. (2003) noted that imprecise estimates are a general feature of change-in-ratio estimators.

13.5 Catch Per Unit Effort Methods

Methods that use both counts of the number of deer harvested and hunter effort (e.g., number of hunters or hunter days) have been used to estimate abundance of deer (e.g., Lancia et al. 1996). This approach is appealing because it simply requires an accounting of the number of deer killed per unit of time (usually by day), which is typically obtained by most state agency deer management programs, and a measure of hunter effort for the same time intervals. Although many state agencies estimate the total number of hunters, and their total effort (i.e., average number of days each licensed hunter pursued deer), they do not estimate hunter effort by day. Thus, most states would require auxiliary surveys of hunters to determine hunter effort by day, which is probably the primary reason why this technique is rarely used in estimating white-tailed deer abundance.

Catch-effort models also have some problems even if daily harvest and hunter effort are available. Defining a unit of hunter effort may be difficult. For example, if hunters can pursue both antlered and antlerless deer they may be equally likely to harvest an antlered deer throughout the hunting season but only harvest antlerless deer later in the season; thus, documenting hunter days may not reflect an accurate measure of hunter effort. Application of a maximum likelihood catch-effort model (Gould and Pollock 1997) to white-tailed deer harvests on a National Guard training facility in Pennsylvania found that model fit was poor for antlerless deer, probably because hunters avoided harvesting antlerless deer in favor of antlered deer until the end of the hunting season (Diefenbach and Vreeland 2005). Changes in hunter behavior (e.g., hunting strategies, weather) violate the assumption of these models that deer vulnerability is constant during the hunting season.

13.6 Population Reconstruction Methods

The simplest population reconstruction methods (e.g., Fry 1949) sum age- and year-specific harvests over time to obtain abundance estimates for a given year. For example, if one sums the number of fawns harvested in year 1, yearlings harvested in year 2, 2-year-olds harvested in year 3, etc. until it is assumed all deer from the cohort in year 1 have died one will obtain an estimate of the number of fawns born in year 1. Of course, this method assumes most mortality is hunting related. Furthermore, population size cannot be estimated for a given year until all deer alive in that year have died. If deer are assumed to survive for 6 years, in the year 2006 the most recent population size that can be estimated is for the year 2001.

To obtain population estimates before all members of a cohort have been harvested, models have been developed that apply past harvest rates to future harvests (that have not yet occurred!). Because these methods assume most mortality is hunting related, they tend to overestimate harvest rates and underestimate population abundance (Roseberry and Woolf 1991). Consequently, if natural or harvest mortality varies over time, these methods will provide inaccurate estimates of abundance (Skalski et al. 2005). Given that winter mortality in Wisconsin is known to be variable (WDNR 2001), most population reconstruction models are unlikely to provide accurate or precise population estimates for the most recent years.

Population reconstruction models commonly used for white-tailed deer include the Wisconsin SAK model, Downing's (1980) backwards reconstruction model, and the Lang and Wood model (Lang and Wood 1976). These types of models usually differ by the assumptions made to estimate harvest rates. An advantage of the Downing model is the ability to reconstruct the prehunt population of the current year using reasonable non-harvest mortality estimates. The weakness of all these types of models is that population estimates for the most recent years are the least accurate. Downing's (1980) model, however, was a "technique of choice" among all models evaluated by Roseberry and Woolf (1991). We compare the Lang and Wood (1976) and Downing (1980) reconstruction models to the Wisconsin SAK model in Section 14.0.

13.7 Statistical Age-at-Harvest Analysis

The shortcoming of traditional population reconstruction methods can be overcome if auxiliary information, such as annual survival, is obtained (Gove et al. 2002). Statistical age-at-harvest methods use a maximum likelihood framework to estimate harvest and survival rates, which permits variance and confidence interval estimation. Furthermore, a suite of models can be constructed to assess, for example, whether survival and harvest rates vary over time or among age-sex classes (Gove et al. 2002, Skalski et al. 2005).

Typically, auxiliary information would be obtained by radiocollaring deer to estimate annual survival and non-hunting mortality. Although this is expensive, and requires radio-collaring studies to be coordinated with long-term population monitoring objectives, it provides empirical information on survival rates. This is preferable to ad hoc adjustments typically employed with age reconstruction methods to account for non-reporting of harvest, crippling loss, and non-hunting mortality (Roseberry and Woolf 1991).

14.0 Comparison of SAK with Downing (1980) Method

Georgia has extensively used a deer population model that is a hybrid of models developed by Downing (1980) and Lang and Wood (1976). In the Downing portion of the model, only antlered bucks are reconstructed because lifetime recovery rates are usually above 0.70 for males (Roseberry and Woolf 1991) but in most cases, female recovery rates are much lower, creating potential for error. The adult buck prehunt estimate from the Downing model is substituted for the Lang and Wood adult buck estimate which is suspect because the average annual reduction rate consistently underestimates mortality (Roseberry and Woolf 1991). The reconstructed buck estimate is multiplied by the unadjusted sex ratio (%1.5 year old bucks/ %1.5 year old does) to estimate adult does. The number of adult does is multiplied by the recruitment rate (fawns in harvest/adult does in harvest) to estimate the prehunt fawn population. The sum of the adult bucks, adult does, and fawns equals the total prehunt population estimate.

In the Downing/Lang and Wood model, sex ratios, buck recovery rates and recruitment rates are determined differently than in the Wisconsin SAK model. Input for both models suffer from potential biases and lack of variance measures that can reduce confidence in the results. We compared the nonstochastic reconstruction models of SAK and Downing/Lang & Wood at nine different DMU's (Table 10) over the time period of 1987-2004 (Figures 19-27). In general, the two methods estimated similar magnitudes of deer abundance and similar time trends with correlations in the range (0.6-0.8). In instances where the correlation between methods was low (0.09-0.37), the abundance was rather constant over time with no obvious trend. On an annual basis, the SAK or Downing/Lang & Wood methods could be either higher or lower with no discernable pattern. There appears to be no obvious bias with one approach. Hence, this analysis suggests no obvious bias nor advantage in substituting the Downing/Lang & Wood method for the current SAK analysis. Results from all reconstruction models can be confounded by changes in age/sex proportions in the harvest produced by special regulations such as point restrictions and earn-a-buck and by hunters who voluntarily become more selective in what they harvest.

15.0 Monitoring Techniques Used by Other State Wildlife Agencies

We surveyed representative states from the Midwest, Southeast, and West seeking information on the type of deer data collected and how they were used to make management decisions. Data collected to facilitate deer management vary considerably among states (Table 8). Approximately two-thirds of the states polled determined harvest through some form of mandatory registration (Table 8); mostly via check stations although telephone checking and mail-back cards were employed by several states. Many biologists consider check stations to be the best method for collecting harvest data because they feel the majority of hunters comply with the checking requirement and, therefore, deer harvest is enumerated (Rupp et al. 2000). However, Virginia noted that mail surveys indicate only 70% of the harvest is registered via check stations (M. Knox, Virginia Department of Game and Inland Fisheries, personal communication), and there are published studies that indicate reporting rates may be low (Hansen et al. in press) and variable even for long-established registration systems (Rosenberry et al. 2004). Most states without mandatory registration estimated harvest through post-season mail surveys (Table 8). Mail surveys are less expensive but in some states sample sizes were inadequate to determine DMU-level harvests. Also, nonresponse by some hunters to the questionnaire may result in biased harvest estimates (Taylor et al. 2000).

Many states have limited resources to collect deer demographic information besides harvest-related data. Approximately one fourth of the surveyed states did not estimate statewide deer population size. Of those that did, most used population reconstruction methods or some variation of the SAK model (Table 9). Over 40% of the states did not estimate DMU-level deer populations or only estimated populations for a limited number of DMUs. Measures of precision and validation of the estimation technique were lacking for nearly all estimates. Some states estimated deer numbers for political or media purposes but population estimates were not used for making management decisions.

Indices of population size and other demographic information were collected by most states although these often were available on geographic or temporal scales insufficient to be useful in making DMU-level management decisions (Table 9). Often, especially in the south, these data were collected only on individual properties with self-imposed harvest restrictions and thus may not have been representative of the DMU or statewide deer population.

Wisconsin is one of the premier white-tailed deer hunting states in the country in terms of number of hunters and number of deer harvested. Wisconsin also has one of the most thorough deer management programs in terms of the harvest and biological data collected and the process developed in using these data to help make deer management decisions. Wisconsin stands out for several reasons. First, many states either do not collect information on deer population status, or collect it in a way that renders it inadequate for making management decisions. Second, Wisconsin has done an excellent job of assessing data needs and developing protocols to collect critical demographic data. Third, Wisconsin thoroughly evaluates the data using models for the scale at which management decisions are made (DMU). Fourth, there is a formalized process by which regional field and central office staff review decisions, especially when adjustments to model input are considered.

Furthermore, in Wisconsin the data collection and analysis process is objective and open to citizen review. The deer management program is clearly defined, well documented, and available to the public (see WDNR 2001). Wisconsin exceeds all states surveyed in the amount of information about the deer management process that is available to their citizens and the transparent manner in which deer management decisions are made.

16.0 General Conclusions

1. Wisconsin has the most comprehensive and transparent deer management program for comparable states that harvest white-tailed deer (Table 9). Wisconsin collects more demographic information, on an annual basis, to monitor the deer population than any of the 21 states surveyed when you consider the following findings (Table 9): (1) nine of 21 states surveyed do not estimate population size by management unit, or only estimate population size for a subset of management units; (2) four of 21 states surveyed do not estimate statewide population size; and (3) few states obtain harvest estimates that account for noncompliance by hunters. The WDNR should be commended for its efforts to track deer population dynamics and make those efforts as transparent as possible.

2. There are several positive aspects of the SAK model as it is applied in Wisconsin. First, the model does reasonably well at estimating N_i at the state-wide level. Second, the model appears relatively robust to changes in female harvest. Third, under stable and nonstationary conditions, there is only minor bias in population estimates. Last, the model allows for an extensive population assessment in contrast to more expensive and intensive procedures, such as sightability models (Samuel et al. 1987), line transect, or mark-recapture.

3. The SAK model appears to be very sensitive to sudden changes in the male harvest rate due to violations in the assumption of a stable and stationary population. Sudden changes in

demography, affect the values of p_{YM} and p_{YF}, resulting in biased abundance estimates. We noted wide changes in SAK estimates compared with simulated known populations as a result of changing male harvest rates. Perhaps most troubling is that the SAK estimates are opposite the true population trend when changes in the male harvest rate are introduced. In contrast, the SAK appears to be more robust to changes in female harvest. Given these findings, any change in regulations that alters the male harvest rate (e.g., earn-a-buck) could drastically bias population estimates. Changes in hunter attitude and hunting styles, such as quality deer management, could further influence SAK estimates given its sensitivity to male harvest rate.

4. The scale of estimation is important and must be considered when evaluating SAK performance. Stochastic demographic processes at small scales (i.e., populations of 10,000) can be relatively large (CV = 12%, $\varepsilon = 0.25$). However, for larger populations, there is relatively less variability. As a consequence, SAK estimates may be precise at the state level, but poor at the DMU level; precise estimation of abundance at the DMU level is not realistic. With both demographic stochasticity and sampling error at DMU levels of effort, the resultant abundance estimates $\left(\hat{N}_i\right)$, were within $\pm 121.9\%$ of the true population level, 95% of the time. The SAK is particularly vulnerable to model violations because of the focus on one age class (1.5 year olds) (i.e., p_{YM} and p_{YF}).

5. The methods used to evaluate the ability of the model to predict future harvests (WDNR 2001) are inappropriate because they do not directly relate to the same scale at which management decisions are made. For 16 DMUs examined, the SAK model explained up to an average of 62% of the variability in the relationship between predicted versus actual harvests among years. However, for some DMUs, the SAK model does a poor job of predicting future harvests. In light of these findings, we recommend that any evaluation of the predictive

capabilities of the SAK model be applied to individual DMUs over time rather than across DMUs. Special attention should be paid to understanding deer harvests and populations in those DMUs where the SAK model predicts poorly over time because it might provide insight for improving deer population modeling in Wisconsin.

Issues of scale also are directly tied to social issues. The number of DMUs in Wisconsin has increased over time in response to demands for more finely tuned management. However, keeping DMUs at a size in which sufficient data can be collected and stochastic variability is small is critically important for population estimation and management recommendations.

6. In northern Wisconsin, precision of $\hat{\lambda}$ is not adequate for precise projections from N_i to N_{i+1}. Although there might be a precise estimate of N_i there always will be a poor estimate of N_{i+1} given the lack of precision in $\hat{\lambda}$. In other words, the precision of N_{i+1} is inherently low because of variability in $\hat{\lambda}$. The rest of Wisconsin does not have a formal model for estimating $\hat{\lambda}$. Hence, we were unable to determine the precision or bias due to $\hat{\lambda}$ for the rest of the state. There is a great need to better understand the relationship between N_i and N_{i+1}. Regression models considering environmental covariates would be helpful in this regard.

7. Occasionally WDNR pools data spatially and temporally for input into the SAK model. Spatial pooling is valid if demographic processes across pooled units are homogenous (meaning that sex and age composition, S_N, S_H, and finite rate of increase are all the same). Careful consideration should be given to differences in harvest regulations across DMUs because regulations could result in heterogeneous demographic processes.

When demographic conditions are homogeneous there are advantages to pooling data. Perhaps most importantly, pooling data increases sample size, which will improve precision of the estimates. At current sampling efforts for age composition and fawn:doe ratios within the DMUs, pooling is necessary to achieve desired levels of precision. Additional benefits of pooling include dampening the influence of demographic stochasticity. We suspect that pooling data at larger spatial scales might account for the precision that has been reported for some large scale investigations of SAK performance.

In conclusion, there is no substitute for direct sampling. Pooling and substituting data is a matter of convenience, providing a cost savings with added risks of additional bias if demographic processes are not stable and stationary.

8. Precision expressions for SAK estimates are currently unattainable given the data used in modeling. Without empirical estimates of all inputs, it is not possible to calculate confidence intervals. Currently, we only have empirical estimates for the following parameters: $\hat{p}_{YM}$, $\hat{p}_{YF}$, $\hat{R}_{J/F}$, and $\hat{\lambda}$ for the northern forested region, but not elsewhere. We do not have empirical estimators or the ability to estimate the variance of the following inputs: θ, $\hat{B}$, and H_i. Skalski and Millspaugh (2002) provided variance expressions for the SAK model if empirical data were available for all input parameters. Given the likelihood of correlation among input parameters, new variance estimators could be derived to incorporate that correlation. However, we would need to know the nature of the correlation among input parameters.

If statistically rigorous measures of precision are desired for population estimates by DMU, the following data are required:

a. Harvest reporting: Compliance by the public is never 100% for any government program and the assumption that all harvested deer are reported, or that a constant proportion of the legal harvest is reported, should be investigated. This would provide empirical data to estimate the proportion of the harvest that is not reported.

b. Buck reporting rate: A statistical model of the buck reporting rate, based on empirical data, will be required. Alternatively, actual estimates of the hunting mortality rate (proportion of all deer killed during the hunting season, whether or not recovered by hunters) could be estimated from a radiotelemetry study of deer.

c. Wounding loss rate: Empirical data to estimate the proportion of the harvest not recovered by hunters are required.

Even if the average number of deer from the antlered and antlerless harvests that were aged each year (in each DMU) did not change, more consistency in the number of deer aged from year to year could potentially reduce the variability in the precision of population estimates.

9. SAK estimates expressed as density based on “available deer range” adds another source of variability, which is important when conveying modeling results to the public. When expressing SAK estimates as density, it requires that available deer range be defined and precisely estimated, which is problematic given differences in habitat quality and various definitions of deer habitat. There is an inherent patchiness in deer range, which likely confuses the public. In addition, variable harvest pressure can affect density distribution. Reporting deer abundance as total numbers (e.g., there are 10,131 deer in a DMU) rather than deer density (e.g., there are 30 deer per square mile) minimizes problems with public perceptions when local abundance appears to deviate from reported densities. It would be advisable to provide SAK abundance estimates rather than density. Uncertainty in the area values also adds variance to the density estimates.

10. The running averages of p_{YM} and p_{YF} produced marginal improvement of SAK performance. Despite only modest improvements to SAK performance, we recommend continued use of three-year running averages. Furthermore, we recommend the use of a weighted average.

11. Given currently available data, it is not possible to make objective adjustments to the buck recovery rate. Given $\hat{B}$ is based on history and intuition without any empirical basis, it is not possible to set criteria or objective rule statements. We recommend $\hat{B}$ be estimated through field studies involving radiotelemetry studies under diverse deer densities, hunter density, number of days hunted, percentage of land accessible to hunters, and weather conditions prior to and during the hunting season.

12. Including July data in the fawn:doe ratio estimates will result in a negative bias because does are still hiding fawns by early July. Therefore only August and September data should be used to estimate $\hat{R}_{J/F}$. Also, the sampling scheme for obtaining these data has potential for bias, for example, it is easiest to obtain a sample in localities with highest density. We recommend that a systematic scheme producing reasonable coverage be considered. We also recommend WDNR initiate an analysis of the extent of variation in fawn:doe ratios and an evaluation of alternative sampling schemes.

13. Seven alternative methods to the SAK model were reviewed as potential methods for estimating deer abundance in Wisconsin. Six of those methods are unlikely to provide more accurate and precise estimates than the SAK model because it is unlikely that critical assumptions of the techniques can be met. It is possible that unrealistic assumptions required in the SAK model (stable and stationary assumption) could be eliminated if auxiliary data were collected to estimate age- and sex-specific harvest rates. These auxiliary data would likely be

expensive to collect because it would require monitoring of radiocollared deer. These data could also be used in alternative estimation methods, such as the statistical age-at-harvest approach (e.g., Gove et al. 2002).

14. Cost is an important consideration for any technique used to monitor wild populations (Skalski 1985, Skalski and Millspaugh 2002). The costs of collecting sufficient data to obtain a statistical measure of precision for all DMUs using Wisconsin's SAK model are likely prohibitively expensive or even logistically impossible. It may be more important to assess the bias in population estimates resulting from violation of model assumptions or from sampling errors (e.g., if methods used to collect data to estimate fawn:doe ratios result in biased estimates).

Cost comparisons between the SAK and other population estimation techniques would be beneficial and should be performed. Reconstruction methods such as the SAK provide a cost effective method for broad scale demographic assessments. In contrast, sightability models (Samuel et al. 1987), distance sampling (Koenen et al. 2002), and mark-recapture are expensive and appropriate only for smaller spatial scales. The combination of multiple data sources, both extensive and intensive might allow for a more rigorous demographic assessment. The relative trade-off between these broad and fine scale methods should be investigated in light of DNR monitoring objectives.

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Table 1. Sixteen Wisconsin Deer Management Units (DMU) for which precision of the Sex-Age-Kill model was evaluated over the years 1986 – 2005.

DMU	Group	Region	Area (sq. miles)	No. deer aged[a]	No. doe and fawns sighted[b]
2	A	Northern Forest	627	114–475	129–993
9	B	Northern Forest	438	148–554	33–654
15	J	Western Farmland	414	263–858	52–285
22	J	Western Farmland	349	125–459	10–105
28	C	Northern Forest	656	17–653	80–670
36	E	Northern Forest	274	165–793	122–1,284
37	E	Northern Forest	235	143–749	38–682
46	K	Eastern Farmland	321	94–333	18–115
49B	H	Northern Forest	182	0–700	11–76
53	L	Central Forest	461	42–439	8–228
55	L	Central Forest	631	6–611	33–259
57A	K	Eastern Farmland	238	185–610	34–192
57C	K	Eastern Farmland	266	15–577	1–139
58	L	Central Forest	506	1–580	9–197
59B	M	Western Farmland	687	121–464	17–132
65A	K	Eastern Farmland	172	1–315	0–100

[a] Range of the number of harvested deer aged each year during the regular firearms season for calculating percent of harvest consisting of 1.5-year-old deer.

[b] Range of the number of doe and fawns sighted each year during summer sighting surveys for calculating the fawn:doe ratio.

Table 2. Mean, minimum, and maximum coefficients of variation (CV) of population estimates for 16 Deer Management Units (DMU) in Wisconsin, 1990–2005.

			CV		
DMU	Group	Region	Mean	Minimum	Maximum
2	A	Northern Forest	15.0	11.6	22.8
9	B	Northern Forest	13.3	11.5	15.8
15	J	Western Farmland	13.7	11.3	19.0
22	J	Western Farmland	15.8	13.3	21.5
28	C	Northern Forest	44.7	13.3	348.9
36	E	Northern Forest	14.6	10.9	23.2
37	E	Northern Forest	13.5	10.9	16.9
46	K	Eastern Farmland	16.6	13.5	22.3
49B[a]	H	Northern Forest	15.9	12.6	19.0
53	L	Central Forest	15.6	13.0	21.3
55	L	Central Forest	14.0	12.4	18.9
57A	K	Eastern Farmland	15.1	12.5	19.6
57C	K	Eastern Farmland	18.9	12.8	30.1
58	L	Central Forest	14.3	11.5	17.6
59B	M	Western Farmland	16.2	13.2	22.2
65A	K	Eastern Farmland	23.4	15.4	44.0

[a] For DMU 49B, population estimates were calculated for the years 1994–2005.

Table 3. Mean, minimum, and maximum CVs for sampling precision for population estimates in 16 Wisconsin Deer Management Units (DMU) when the age structure is retained from the original data but sample sizes are held constant for the number of deer aged from the antlered and antlerless harvest.

	Age 600 deer from antlered harvest per year per DMU			Age 600 deer from antlerless harvest per year per DMU			Age 600 deer each from antlered and antlerless harvest per year per DMU		
DMU	$\bar{x}$	Minimum	Maximum	$\bar{x}$	Minimum	Maximum	$\bar{x}$	Minimum	Maximum
2	14.3	12.1	17.7	11.9	9.4	20.1	11.1	9.3	17.1
9	12.8	12.8	15.2	11.5	9.5	13.8	10.8	9.3	12.8
15	13.7	13.7	18.7	12.7	10.2	18.1	12.6	10.3	17.0
22	15.8	15.8	20.8	13.7	11.8	17.5	13.4	11.1	18.2
28	23.2	23.2	55.3	17.1	10.1	48.6	12.8	9.5	23.4
36	13.8	13.8	18.3	13.1	9.0	21.2	11.9	9.2	16.5
37	13.1	13.1	15.0	11.8	10.0	15.9	11.3	9.5	13.7
46	16.4	16.4	21.5	13.4	10.8	19.5	13.0	10.3	18.7
49B[a]	15.6	15.6	19.8	13.8	11.1	17.9	14.0	10.6	18.0

53	15.3	15.3	21.3	13.7	11.6	18.0	13.2	10.9	18.3
55	13.8	13.8	18.5	11.9	10.1	15.9	11.7	9.9	15.6
57A	15.1	15.1	20.4	13.1	10.9	16.2	12.9	11.1	16.1
57C	18.8	18.8	30.0	17.5	11.9	29.4	17.3	11.6	30.4
58	14.4	14.4	18.4	12.9	10.3	16.7	13.2	10.5	17.3
59B	16.2	16.2	22.6	13.8	11.8	18.5	13.6	11.6	18.8
65A	22.9	22.9	46.3	20.9	12.4	45.3	20.4	12.3	45.6

Table 4. Mean, minimum, and maximum CVs for population estimates in 16 Wisconsin Deer Management Units (DMU) when the fawn:doe ratio is retained from the original data but sample sizes are increased and held constant for the number of deer sighted during summer surveys.

	Sight 100 adult females and fawns per year per DMU			Sight 200 adult females and fawns per year per DMU			Sight 400 adult females and fawns per year per DMU		
DMU	$\bar{x}$	Minimum	Maximum	$\bar{x}$	Minimum	Maximum	$\bar{x}$	Minimum	Maximum
2	15.7	12.9	22.8	15.6	13.2	23.9	15.4	12.8	22.6
9	13.9	11.9	17.7	14.1	11.5	17.6	13.7	11.1	17.5
15	15.3	10.3	24.9	15.1	10.5	24.4	15.1	11.1	25.2
22	15.9	12.6	26.8	15.6	12.8	25.8	15.5	12.3	25.9
28	26.7	13.1	71.7	27.6	12.6	77.5	26.6	13.2	56.8
36	15.4	10.8	23.8	15.3	10.8	24.3	15.2	10.8	22.4
37	13.9	11.4	16.4	13.8	11.2	16.3	13.8	11.4	16.6
46	17.6	12.8	25.6	17.5	13.2	25.8	17.3	12.9	24.5
49B[a]	15.2	11.1	21.5	15.3	11.4	22.1	15.0	11.2	21.3

53	15.6	12.1	26.5	15.5	12.1	26.4	15.5	11.6	26.2
55	14.0	11.7	20.6	14.2	11.7	21.3	14.0	12.1	20.4
57A	15.9	11.8	23.1	16.1	12.1	23.0	16.2	12.3	23.3
57C	16.0	12.0	19.8	15.9	11.4	20.4	15.8	11.4	20.1
58	14.8	11.7	19.6	14.7	11.2	19.6	14.9	11.9	19.7
59B	17.6	12.4	29.1	17.3	13.3	28.0	17.2	12.9	28.0
65A	18.6	14.3	26.1	18.4	14.3	25.0	18.7	14.4	25.7

Table 5. Pearson product-moment correlation coefficients of the recorded buck harvest with the previous year's recorded buck harvest and SAK predicted buck harvest for 1992-2005 using data from 16 selected deer management units each year.

	Correlation with	
Year	Predicted buck harvest	Previous year's buck harvest
1992	0.97	0.91
1993	0.95	0.95
1994	0.97	0.96
1995	0.94	0.96
1996	0.88	0.96
1997	0.87	0.97
1998	0.83	0.95
1999	0.97	0.97
2000	0.95	0.96
2001	0.89	0.97
2002	0.81	0.91
2003	0.93	0.93
2004	0.91	0.97
2005	0.87	0.97

Table 6. Pearson product-moment correlation coefficients of the recorded buck harvest with the previous year's recorded buck harvest and SAK predicted buck harvest for 16 selected deer management units (DMU) during the years 1992-2005.

	Correlation with	
DMU	Predicted buck harvest	Previous year's buck harvest
2	0.73	0.36
9	0.59	0.38
15	0.56	0.27
22	0.56	0.41
28	0.08	0.24
36	0.79	0.75
37	0.68	0.57
46	0.65	0.63
49B	0.62	0.59
53	0.77	0.53
55	0.77	0.32
57A	0.63	0.41
57C	0.75	0.52
58	0.84	0.63
59B	0.51	0.22
65A	0.35	0.39

Table 7. Summary table of alternative population estimation methods.

Estimation technique	Data collection methods	Advantages	Disadvantages or problems
Index methods	Some environmental or other measure (e.g., pellet counts, buck kill per square mile, etc.) is assumed to be proportional to true abundance over time	• Data are usually relatively inexpensive to obtain or easily collected	• Does not provide a direct estimate of abundance • Few indices have been validated as directly correlating with abundance • Must assume that the proportional relationship between the index and true abundance is constant over time
Distance sampling	Roadside surveys of deer, usually performed as spotlight surveys	• Does not require capturing and marking animals • Provides a direct estimate of abundance • Can be conducted any time of year • Relatively inexpensive	• Likely obtain biased estimates because counting deer along roads does not represent a random sampling of the environment • Surveys usually have to be conducted in winter because of less visual obstruction by vegetation • Cannot distinguish between antlered and antlerless deer in winter • Provides minimal information on the age structure of the population

Table 7, cont.

Estimation technique	Data collection methods	Advantages	Disadvantages or problems
Aerial surveys using sightability models	A marked sample of deer is used to develop a model to estimate the probability a deer is detected. Future aerial surveys use this model to adjust survey counts for missed deer	• Once a sightability model is developed the technique does not require marked animals • Provides direct estimate of abundance	• Developing a sightability model requires radio-collaring deer and is expensive • The resulting sightability model is assumed to be applicable to all future aerial surveys • Surveys usually have to be conducted in winter because of less visual obstruction by vegetation • Cannot distinguish between antlered and antlerless deer in winter • Aerial surveys can be expensive and aircraft accidents are the leading occupation-related mortality factor for wildlife biologists
Change-in-ratio	Pre- and post-hunt visual surveys are conducted and the number of deer removed from the population (harvested) is recorded	• Does not require capturing and marking deer • Harvest data are readily obtained • Pre- and post-harvest surveys can be readily implemented	• The probability of detecting antlered and antlerless deer is known to differ for visual surveys, and the technique assumes both types of deer have equal probability of detection. • The change-in-ratio technique is not robust to violation of this assumption

Table 7, cont.

Estimation technique	Data collection methods	Advantages	Disadvantages or problems
Catch-effort	Both harvest and hunting effort (e.g., number of hunters, hunter days, etc.) data are collected	• Does not require capturing and marking deer • Harvest and hunter effort data are readily obtained	• The vulnerability of deer is assumed not to change during the hunting season • The number of hunters, or hunter hours, may not accurately reflect hunter effort because hunters may be more likely to harvest bucks early in the season and antlerless deer later in the season • A large proportion of the population (>30%) must be harvested annually to accurately estimate population size
Sex-age-kill Lang and Wood	Number of deer harvested and age-sex structure of the harvest are the primary data needed. Auxilliary data can be incorporated into the model	• Does not require capturing and marking deer • Harvest data are readily obtained	• Assumes all antlered deer have same probability of harvest • Assumes a stable and stationary population unless auxiliary data are collected

Table 7, cont.

Estimation technique	Data collection methods	Advantages	Disadvantages or problems
Population reconstruction models	Number of deer harvested and age-specific harvest rates	• Does not require capturing and marking deer • Harvest data are readily obtained	• Assumes most mortality is harvest-related • Must wait until all age classes of a given cohort are harvested before population size can be estimated • Assumes constant age-specific harvest rates for harvests that have not yet occurred • Changes in harvest regulations can bias population estimates
Statistical age-at-harvest analysis	Number of deer harvested and auxiliary demographic information	• Based primarily on harvest data • Harvest data are readily obtained • Provides statistical measures of precision	• Auxilliary data likely will require capturing and radio-collaring deer • Radio-tagging studies must be designed to be compatible with long-term population monitoring objectives • Radio-tagging studies are expensive and this approach is even more expensive if these studies must be replicated across a state with demographically diverse deer populations.

Table 8. Harvest and hunter statistics for white-tailed deer for selected states.

State	Land area (sq. miles)	2004 Harvest		Total harvest per sq. mile	Number of hunters		Firearms hunters per sq. mile
		Archery	Firearms		Archery	Firearms	
AL [a]	50,744	51,343	483,749	10.5	74,456	229,420	4.5
AR [a]	52,068	13,043	117,891	2.5	87,000	241,956	4.6
GA [a]	57,906	57,600	426,400	8.4	96,844	279,382	4.8
IN	35,867	22,005	101,053	3.4	99,158	159,130	4.4
IL	55,584	63,639	126,817	3.2	120,000	200,000	4.1
IA	55,869	23,941	158,915	3.3	52,078	154,036	2.8
KS	81,815	8,200	64,300	0.9	21,780	68,453	0.8
MA	7,840	3,045	8,693	1.5	23,862	55,000	7.0
ME	33,215	2,084	28,842	1.1	14,295	183,000[b]	5.5
MN	79,610	21,700	268,300	3.6	70,000	500,000	6.3
MS	46,907	33,968	248,482	6.0	40,413	107,463	2.3
MO	68,886	33,526	254,814	4.2	150,000	475,000	6.9
NY	47,214	29,775	178,631	4.4	206,925	568,092	12.0
OH	40,948	50,564	147,226	4.8	250,000	400,000	9.8
PA	44,817	65,100	399,790	10.4	282,100	730,000	16.3
SC	30,109	15,078	258,426	9.1	27,852	139,437	4.6
TN	41,217	19,935	141,845	3.9	82,554	188,608	4.6
TX	261,797	13,008	418,314	1.6	70,905	506,353	1.9
VA	39,594	17,134	219,901	6.0	60,000	320,000	8.1
WV	24,078	26,227	152,839	6.3	153,793	290,000	12.0
WI	54,310	95,607	388,344	8.9	250,000	650,000	12.0

[a] Harvest data are from 2003.

[b] Does not include shotgun/muzzleloader season.

Table 9. Methods of estimating hunter harvest, population size, indices used to monitor population trends, and demographic characteristics used to monitor white-tailed deer for selected states in the eastern and midwestern U.S.

State	Primary Method of Determining Harvest	Method of Estimating Population Size[a]		Trend Indices[c]	Demographic Information	
		Statewide	Management Unit		Type	How Often Collected
AL	Mail survey				Fecundity	Periodically
AR	In-person registration			B,C	Fecundity Condition	Annually Annually
GA	Telephone survey	Reconstruction/ Lang & Wood	Reconstruction/ Lang & Wood	A,B,E	Age structure & Condition	Annually
IN	In-person registration			A,B,E	Age structure	Annually
IL	Telephone	Reconstruction	Reconstruction	A,B,C,D	Fecundity Mortality Age structure	Periodically Annually Annually
IA	Mail survey	Reconstruction	Reconstruction	A,B,D,F	Fecundity	Annually
KS	Mail survey	Reconstruction Spotlight survey	Spotlight survey	A,B,C	Age structure	Annually
MA	In-person registration	Reconstruction	Reconstruction	B	Condition Age structure	Annually Annually
ME	In-person registration	SAK model	SAK model	A,B,C	Condition Age structure Winter severity Fecundity/Recruitment	 Annually Annually Annually
MN	In-person registration	Reconstruction	Reconstruction Aerial survey	B	Fecundity	Annually
MS	Mail survey	SAK model[b]			Fecundity Recruitment	Periodically Periodically
MO	Telephone	Reconstruction	Reconstruction	A,B,C	Fecundity Mortality Age structure	Periodically Periodically Annually
NY	Telephone	SAK model		B,C	Condition Age structure	Annually Annually

Table 9. Continued.

State	Primary Method of Determining Harvest	Method of Estimating Population Size[a]		Trend Indices[c]	Demographic Information	
		Statewide	Management Unit		Type	How Often Collected
OH	In-person registration	SAK model Reconstruction	SAK model[b] Reconstruction	A,B	Fecundity Recruitment Condition	Periodically Annually Annually
PA	Mail-in Cards	SAK model	SAK model		Fecundity Mortality Age structure Winter severity	Annually Periodically Annually Annually
SC	Mail survey	SAK model		B	Fecundity Mortality	Periodically Periodically
TN	In-person registration			B,E	Fecundity Age structure Condition	Annually Annually Annually
TX	Mail survey	Spotlight surveys	Spotlight surveys	B,D	Age structure Fecundity Browse surveys Herd health	Annually Periodically Annually Periodically
VA	In-person registration			B	Fecundity Condition Age structure	Annually Annually Annually
WV	In-person registration	SAK model	Reconstruction[b]	A,B,C,E	Fecundity Condition Age structure	Periodically Periodically Annually
WI	In-person registration	SAK model	SAK model	A,B	Fecundity Recruitment Condition Age structure Winter severity	Periodically Annually Annually Annually Annually

[a] Includes accounting type models

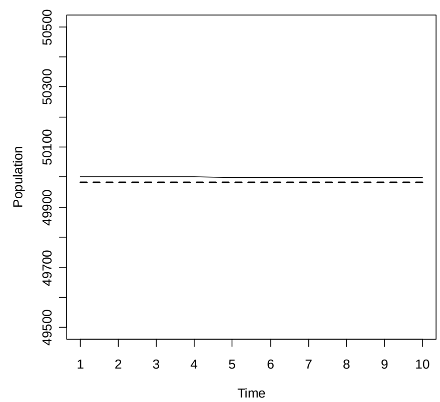
[b] For selected units only

[c] A = Deer-vehicle collisions; B = Hunter harvest; C = Bowhunter observations; D = Spotlight surveys; E = Crop damage complaints; F = Aerial surveys

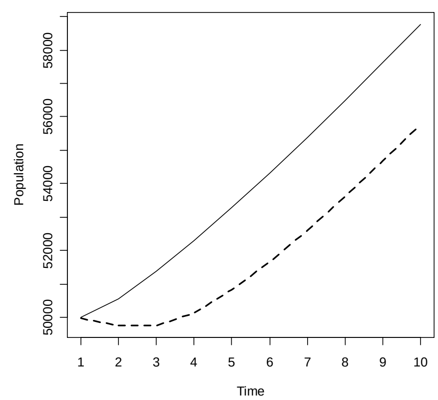
Table 10. Correlation (*r*) between SAK and Downing/Lang and Wood estimates of total prehunt white-tailed deer abundance at nine different DMU's for the period 1987-2004.

DMU	*r*
15	0.6619
22	0.6098
46	0.6990
53	0.1542
55	0.5630
57A	0.3674
57C	0.7048
59B	−0.0919
65A	0.8531

a. Stable-stationary



b. Stable, $\lambda > 1$



c. Stable, $\lambda < 1$

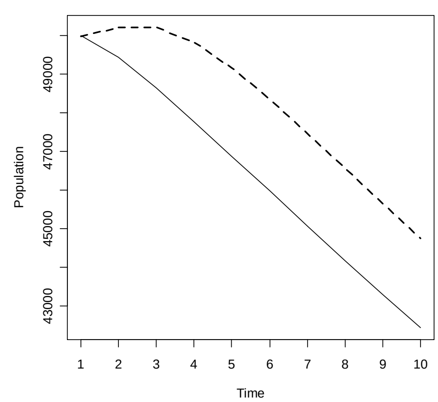
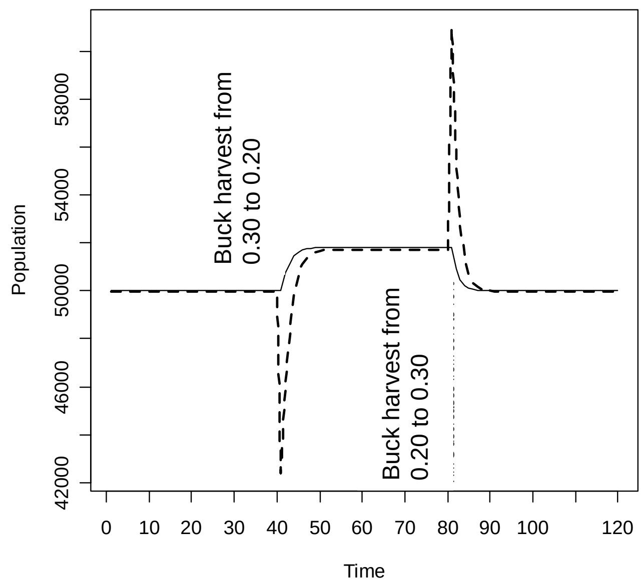


Figure 1. Illustration of population trends and corresponding SAK model estimates of abundance $\left(\hat{N}_i\right)$ under (a) stable-stationary, (b) stable-nonstationary $(\lambda > 1)$, and (c) stable-nonstationary $(\lambda < 1)$ demographic conditions. Results based on a deterministic, two-sex Leslie matrix model. True abundance (solid line ——), SAK estimates (dashed line ----).

a. SAK based on annual estimates of p_{YM} and p_{YF}



b. SAK based on three-year running averages of p_{YM} and p_{YF}

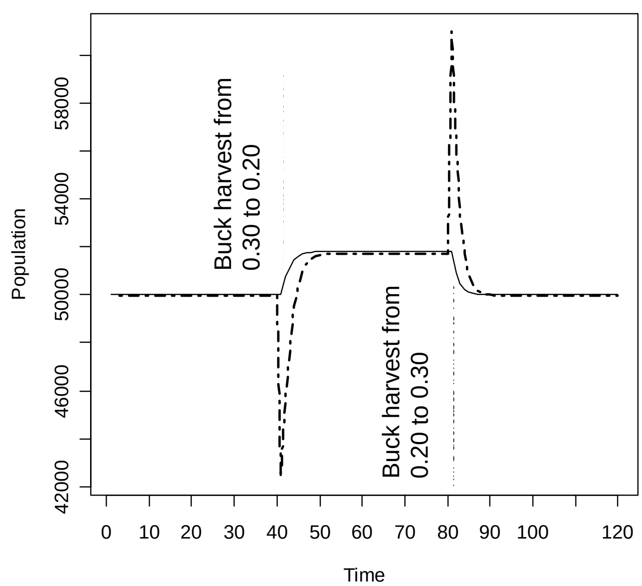


Figure 2. Illustration of population trends and corresponding SAK model estimates of abundance, N_i, followed by a 0.10 decline in buck harvest rate, followed by a 0.10 increase in buck harvest rate. Results based on a deterministic, two-sex Leslie matrix model. Modelled abundance (solid line——) and SAK estimates (dashed line ----). The population was generated using the Leslie two-sex model under stable and stationary conditions for the first 40 years. In year 41, the buck harvest rate

was changed from a probability of 0.30 to 0.20, and remained so for the next 40 years (years 41-80). During that period, the population achieved a different set of stable and stationary conditions. Then in year 81, the buck harvest reverted back to the original rate of 0.3. Then the population reached a new stable and stationary condition over years 81-120, the same as the original set of conditions at the beginning of the simulation. The population trend is plotted by the solid line. The corresponding annual SAK estimates are plotted by the dashed line

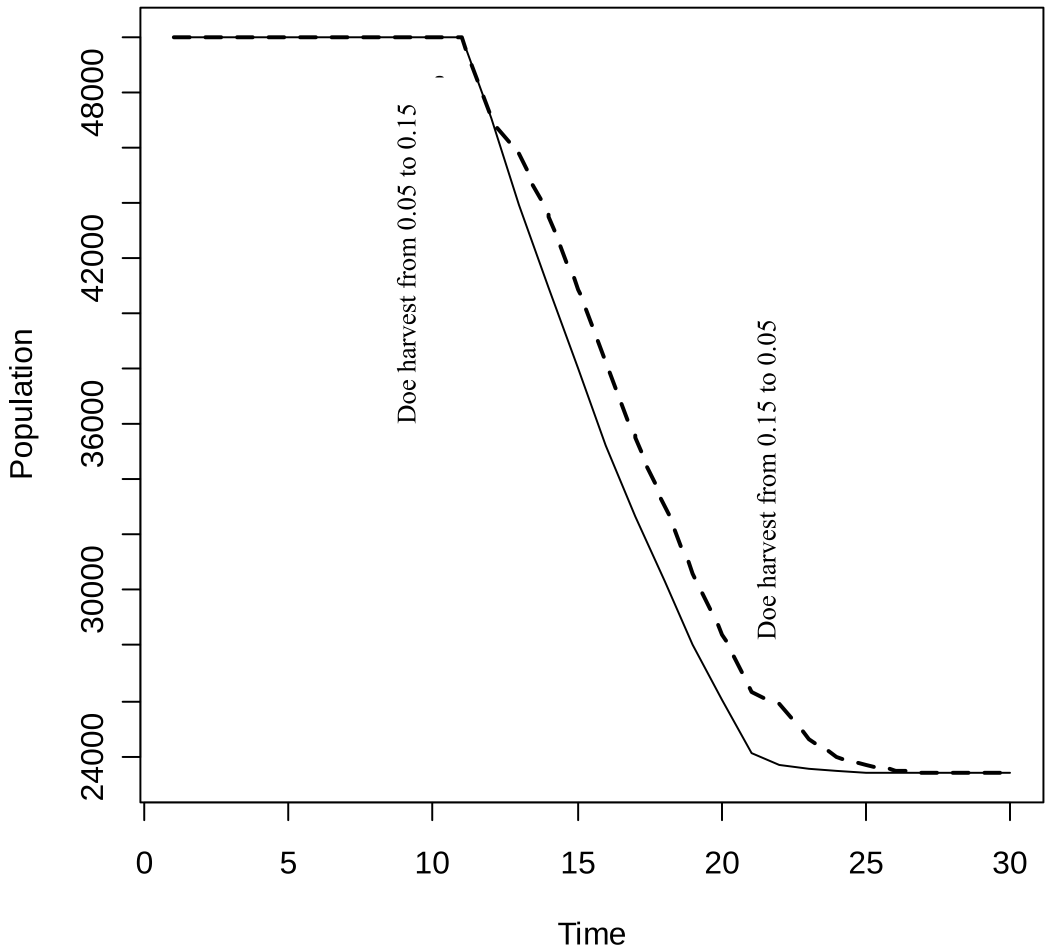
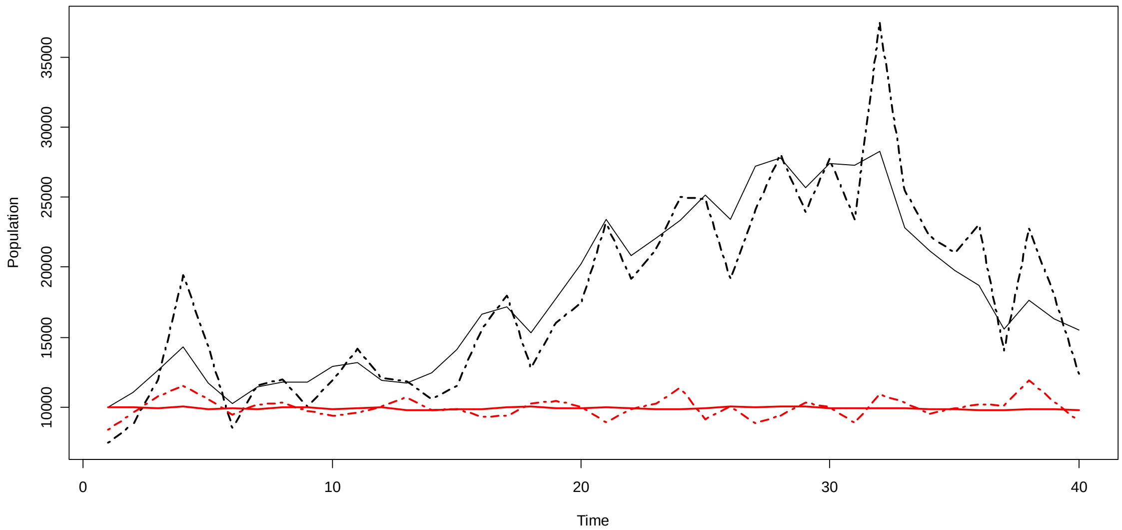


Figure 3. Illustration of population trends and corresponding SAK model estimates of abundance, N_i, under a stable-stationary condition, followed by a 0.10 increase in doe harvest rate. Results based on a deterministic, two-sex Leslie matrix model. Simulated abundance (solid line ___), SAK estimates (dotted line ----).

a.



b.

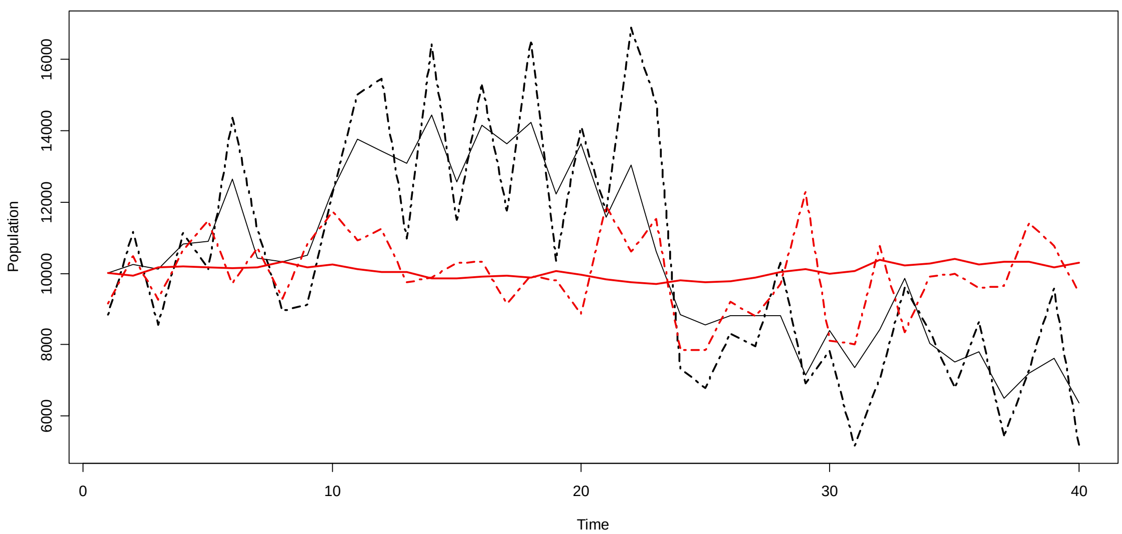


Figure 4. Two examples of 40 years of Leslie matrix population simulations (solid lines) and associated SAK estimates (dashed lines) for the case of no correlation between annual natural survival and productivity (i.e., $\varepsilon = 0$, red lines) and positive correlation $\left(\varepsilon \sim U\left(-0.2, +0.2\right),\ \text{black lines}\right)$. Note both the variance in simulated abundance and sampling error in the SAK model increase with positive correlation.

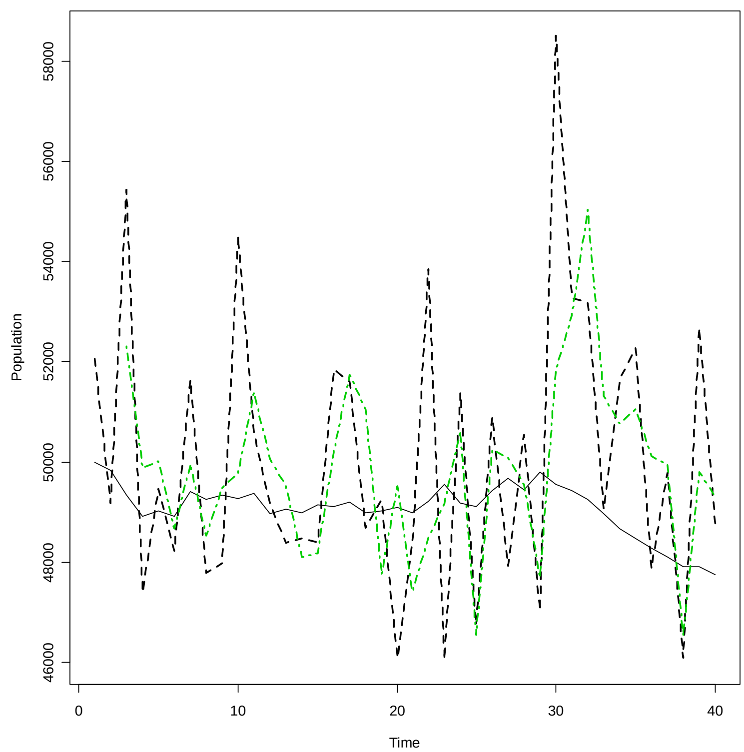


Figure 5. Comparison of SAK estimates of $\hat{N}_i$ based on one-year (i.e., current year) or three-year moving average estimates of $\hat{p}_{YM}$ and $\hat{p}_{FM}$ in the presence of stochastic demographic variability. Results based on a stochastic, two-sex Leslie matrix model with binomial survival and harvest, and Poisson recruitment. Abundance from the projection matrix model with independent vital rates (solid line _____), one-year SAK (dash and dotted line, green), and moving average (-----).

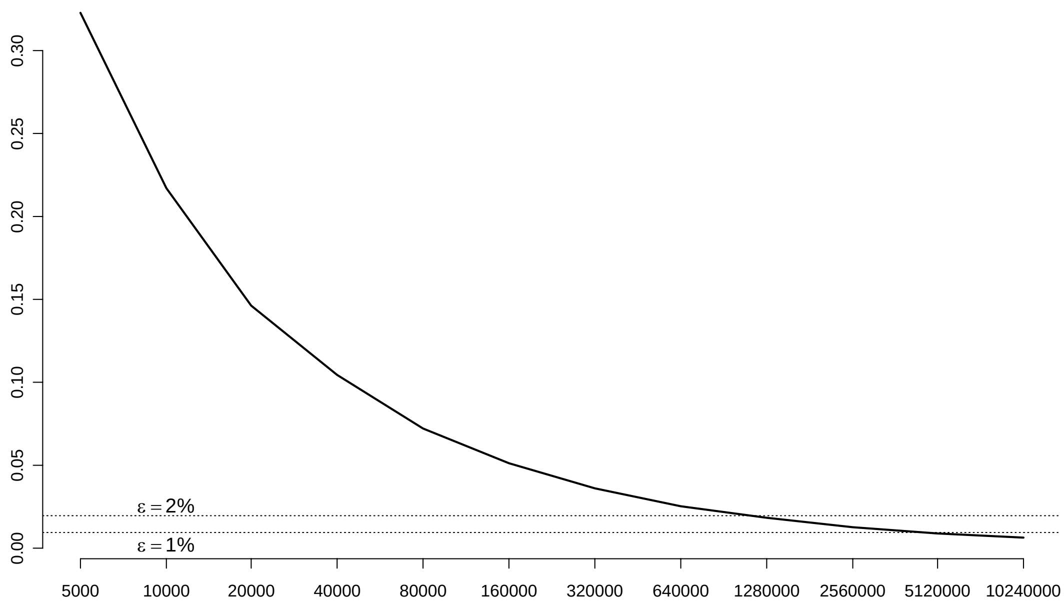


Figure 6. The error in SAK estimation (ε = 1.96 CV) versus population size. This stochastic variability is based on calculating SAK values with *exact* demographic values (i.e., no sampling error).

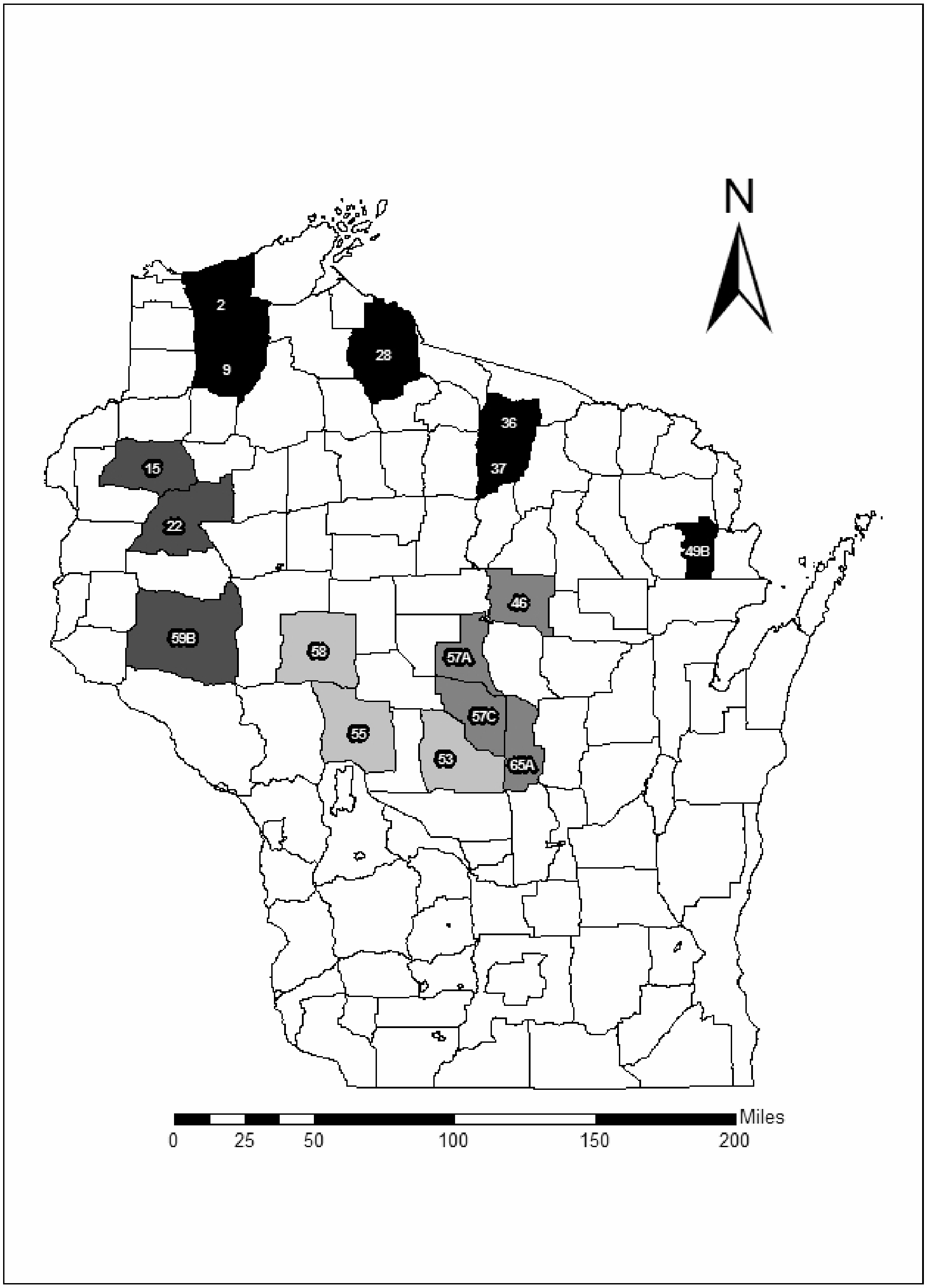


Figure 7. Sixteen Deer Management Units for which data were used to estimate the precision of Wisconsin Sex-Age-Kill population estimates.

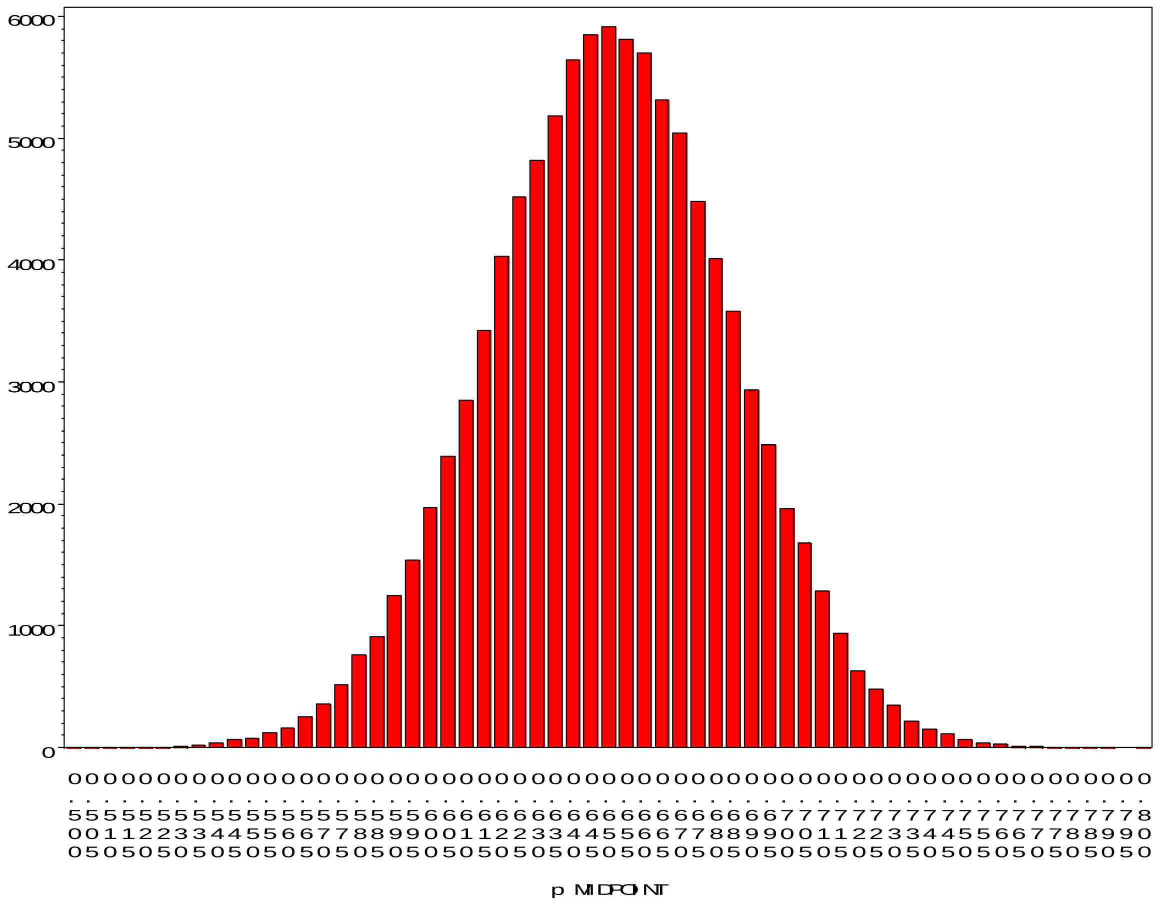
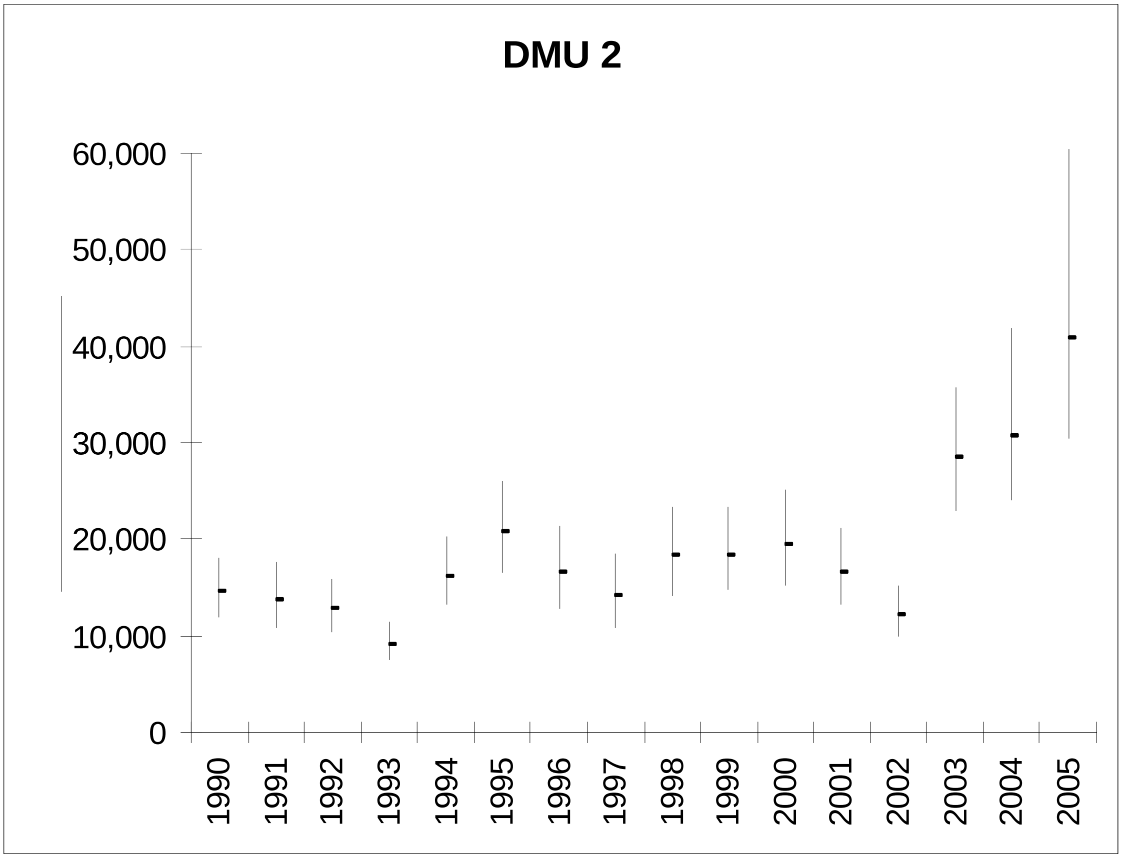


Figure 8. Distribution of a binomial random variable (e.g., proportion of 18-month-old males observed in a sample of deer from the antlered harvest) with a mean of 0.65 and sample size of 200.



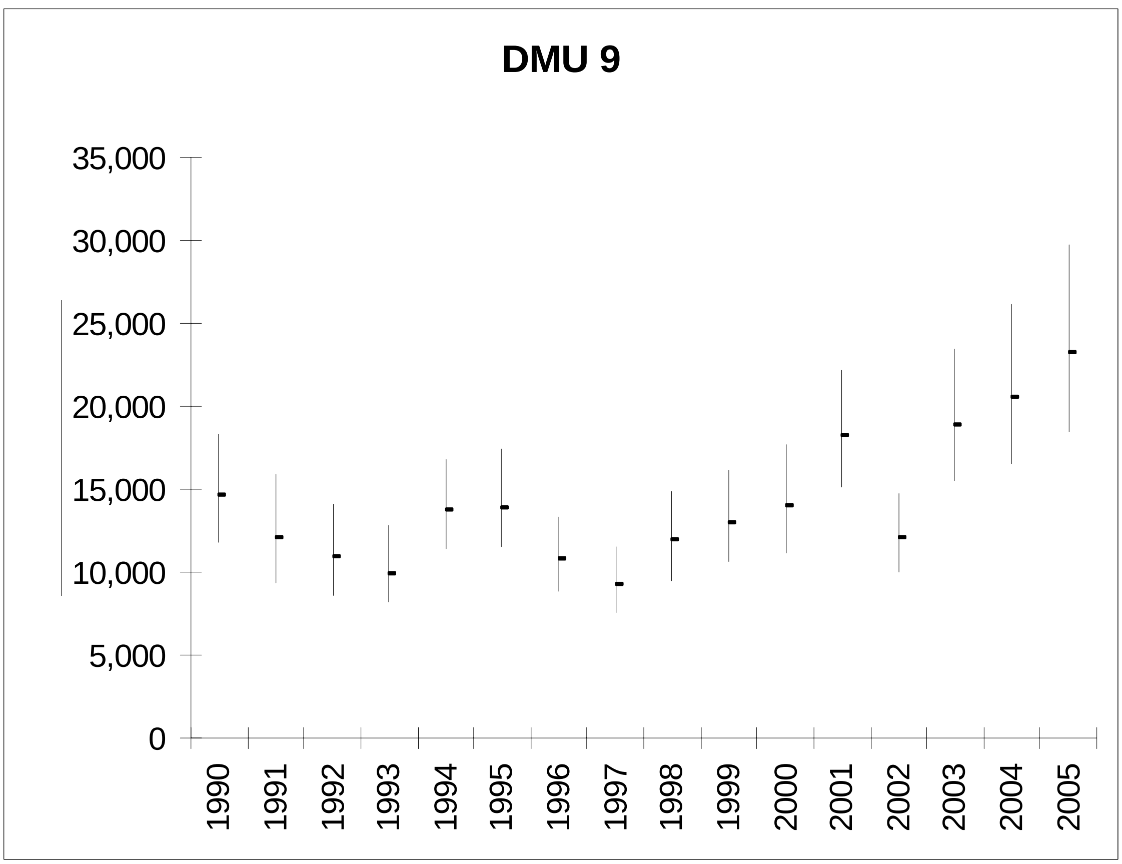
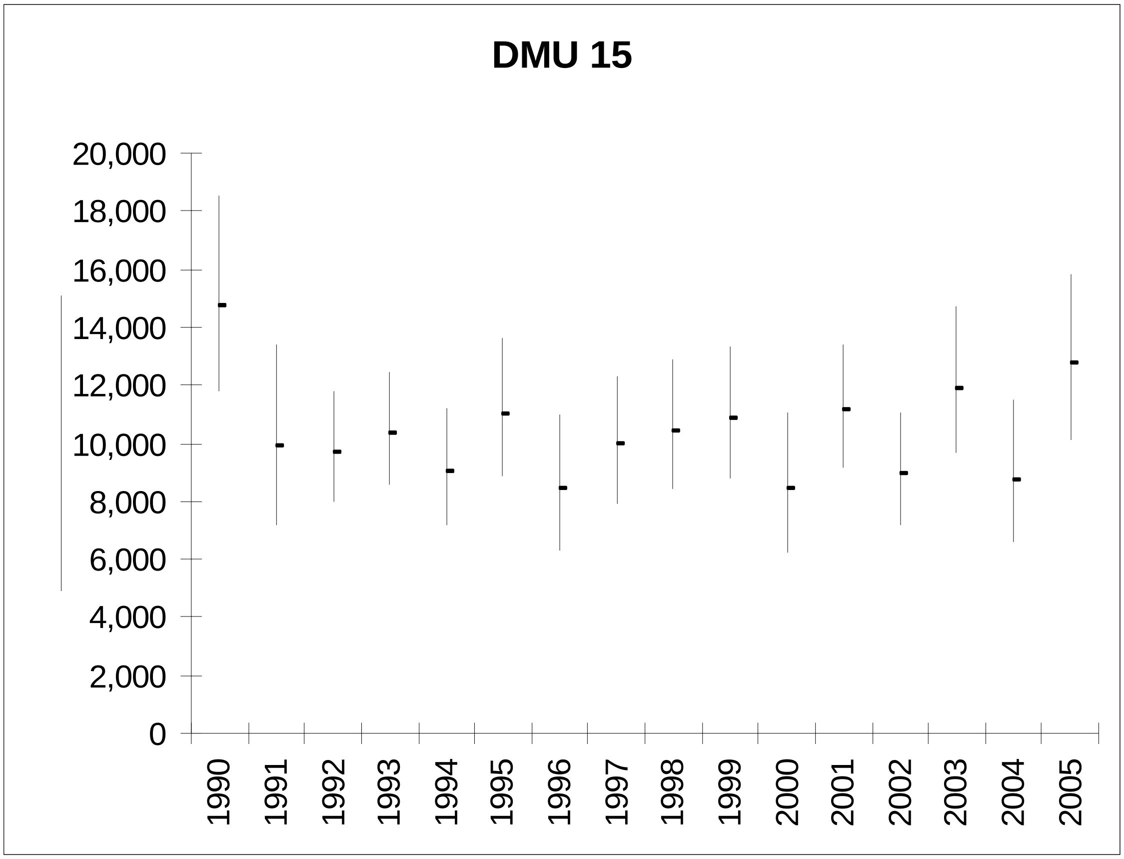


Figure 9. Population estimates and 90% confidence intervals, for the Wisconsin Sex-Age-Kill model, for white-tailed deer populations in Deer Management Units (DMU) 2 and 9, 1990–2005.



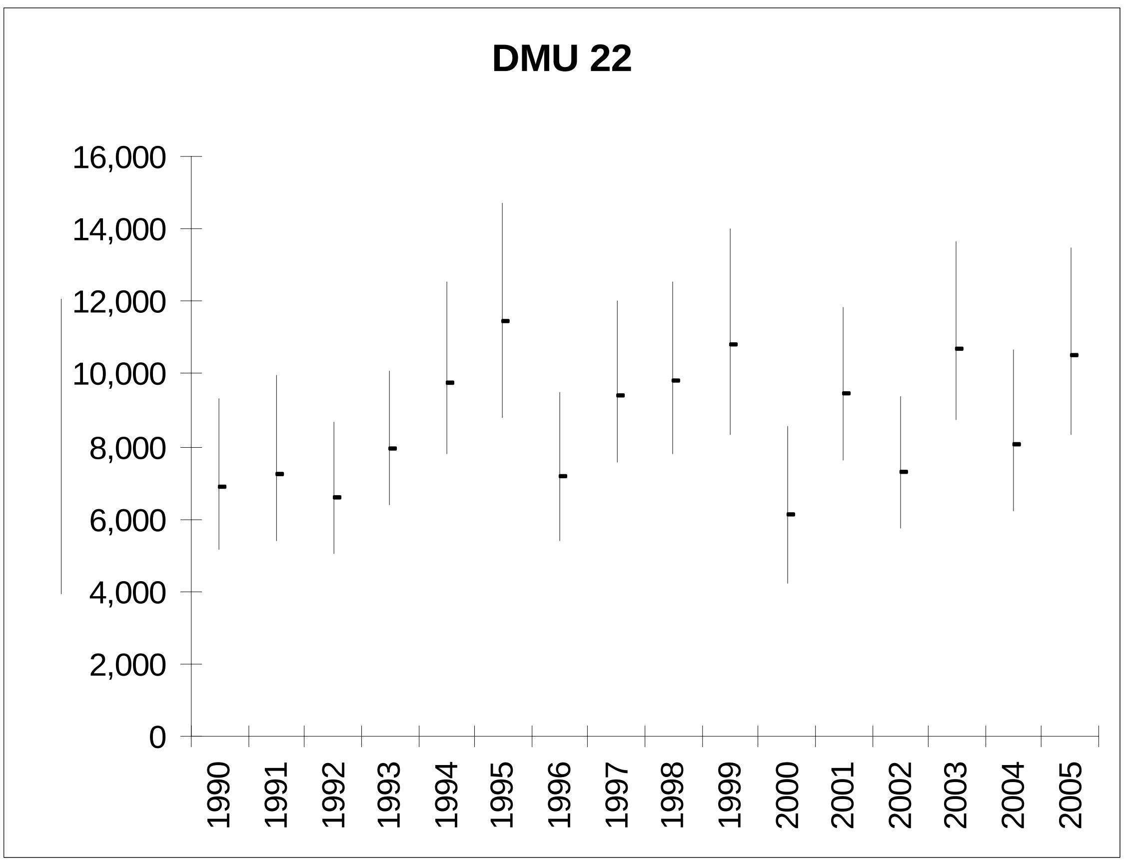
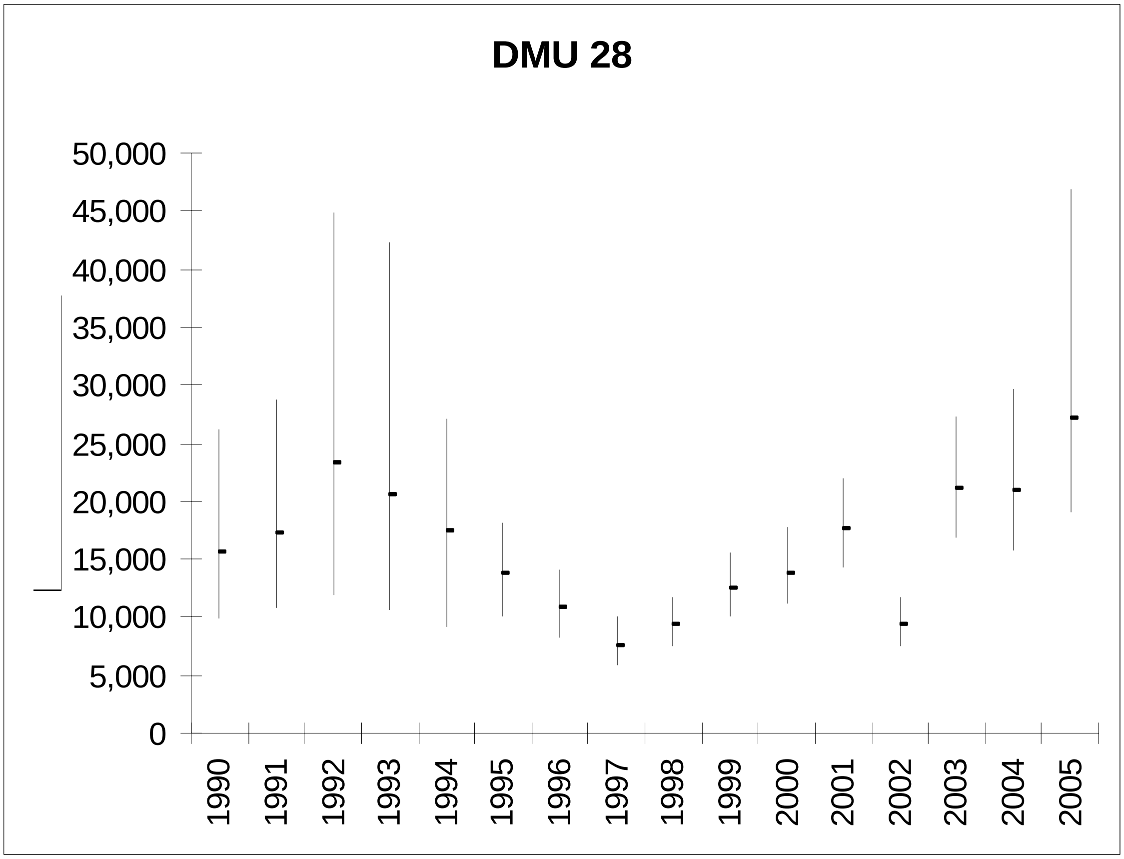


Figure 10. Population estimates and 90% confidence intervals, for the Wisconsin Sex-Age-Kill model, for white-tailed deer populations in Deer Management Units (DMU) 15 and 22, 1990–2005.



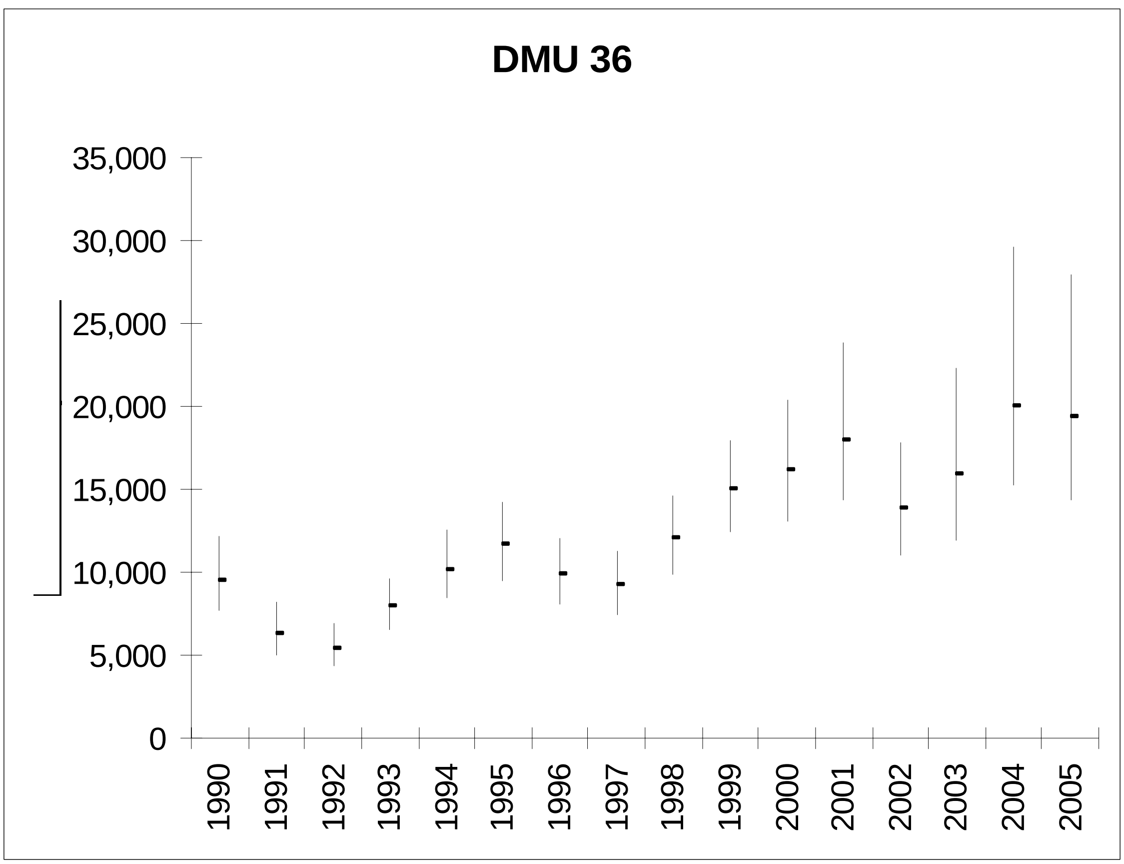
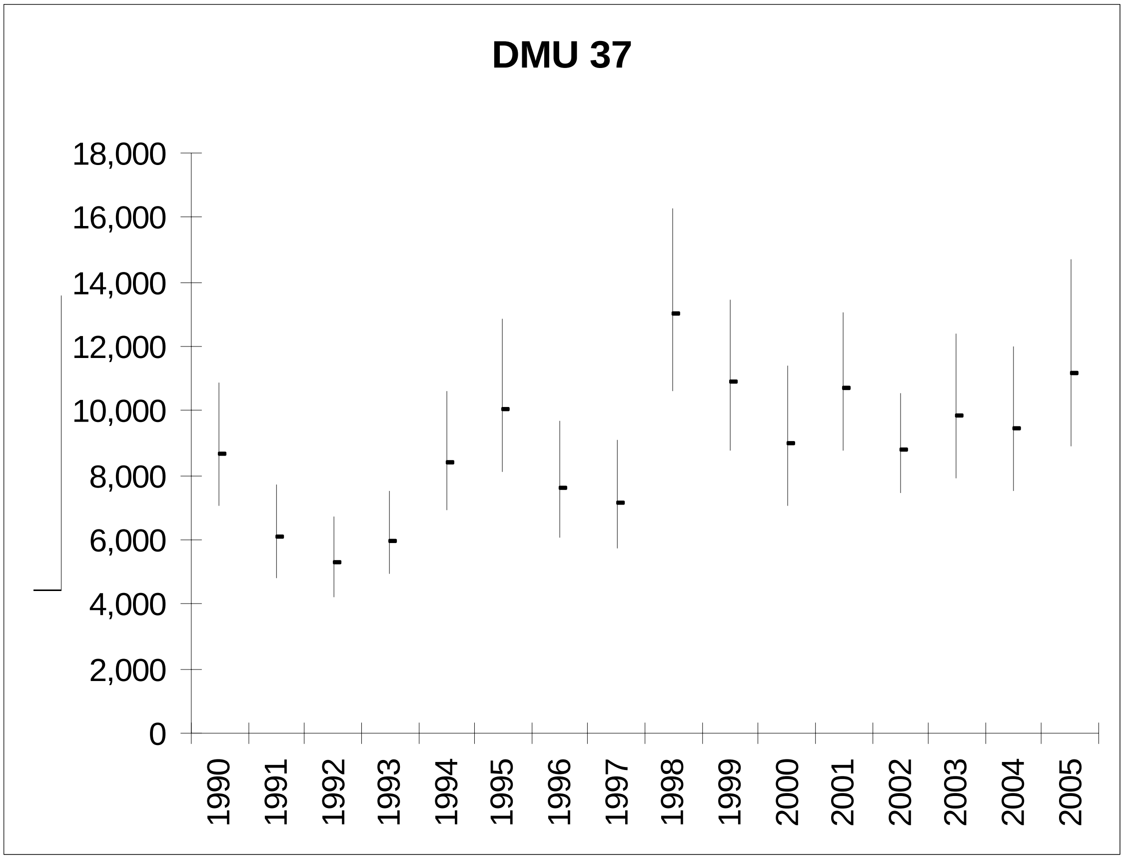


Figure 11. Population estimates and 90% confidence intervals, for the Wisconsin Sex-Age-Kill model, for white-tailed deer populations in Deer Management Units (DMU) 28 and 36, 1990–2005.



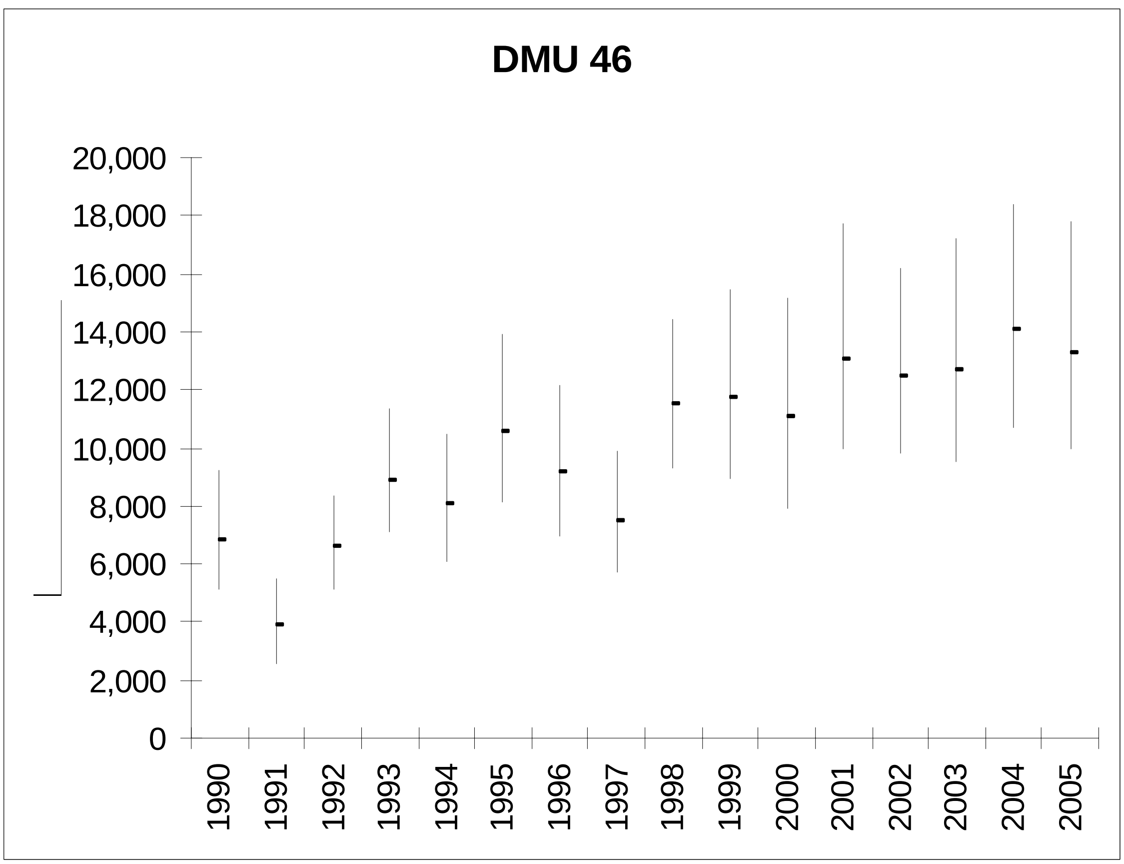
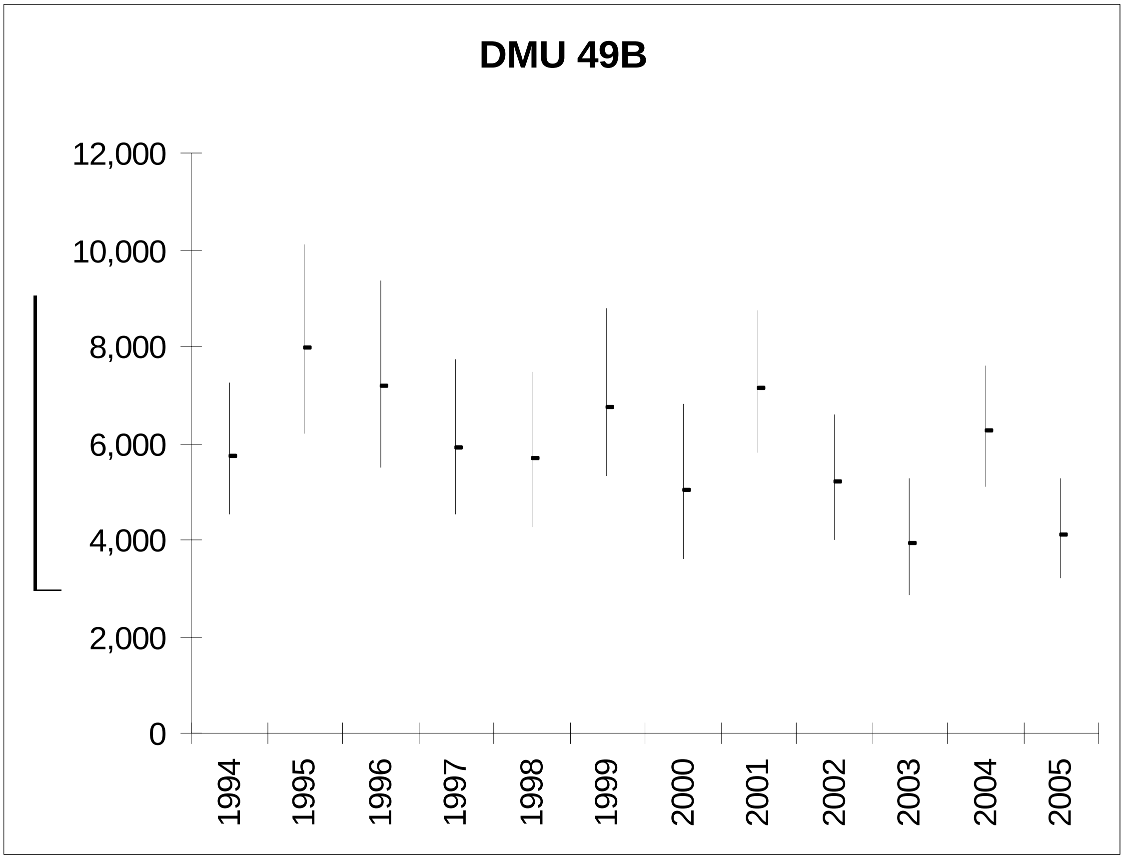


Figure 12. Population estimates and 90% confidence intervals, for the Wisconsin Sex-Age-Kill model, for white-tailed deer populations in Deer Management Units (DMU) 37 and 46, 1990–2005.



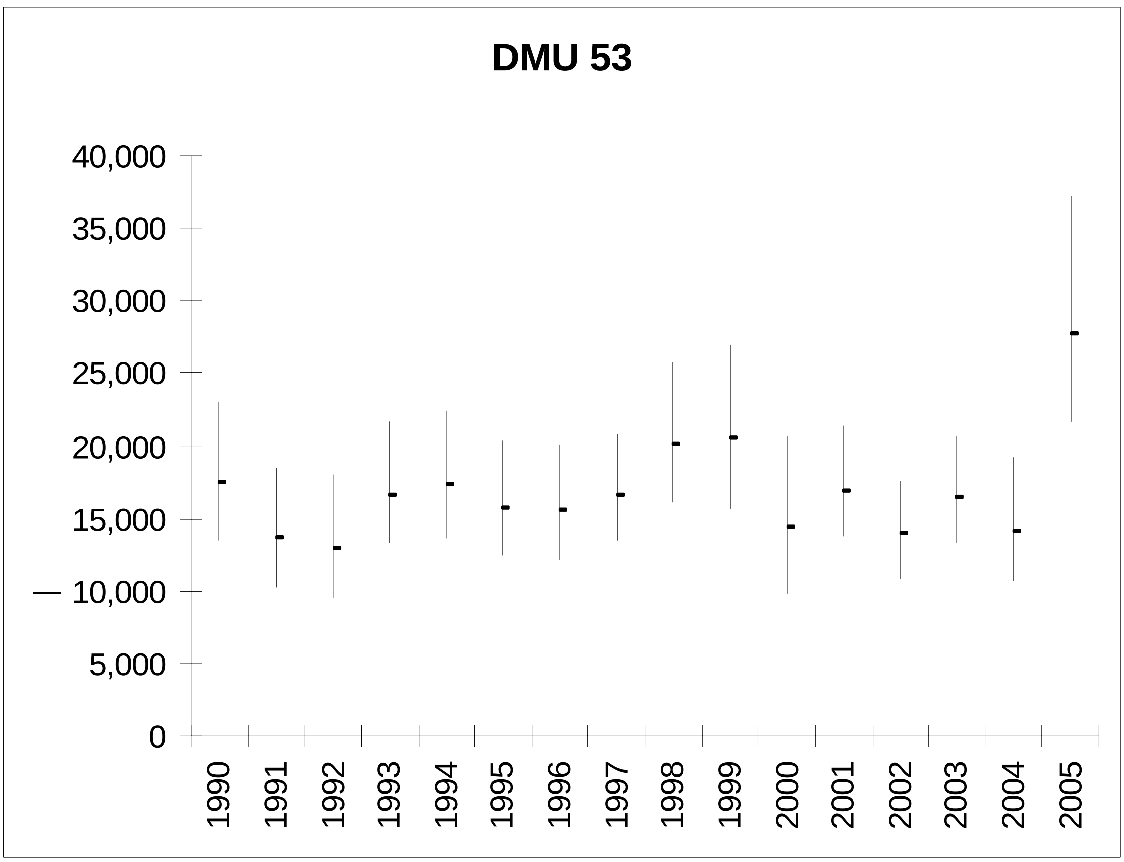
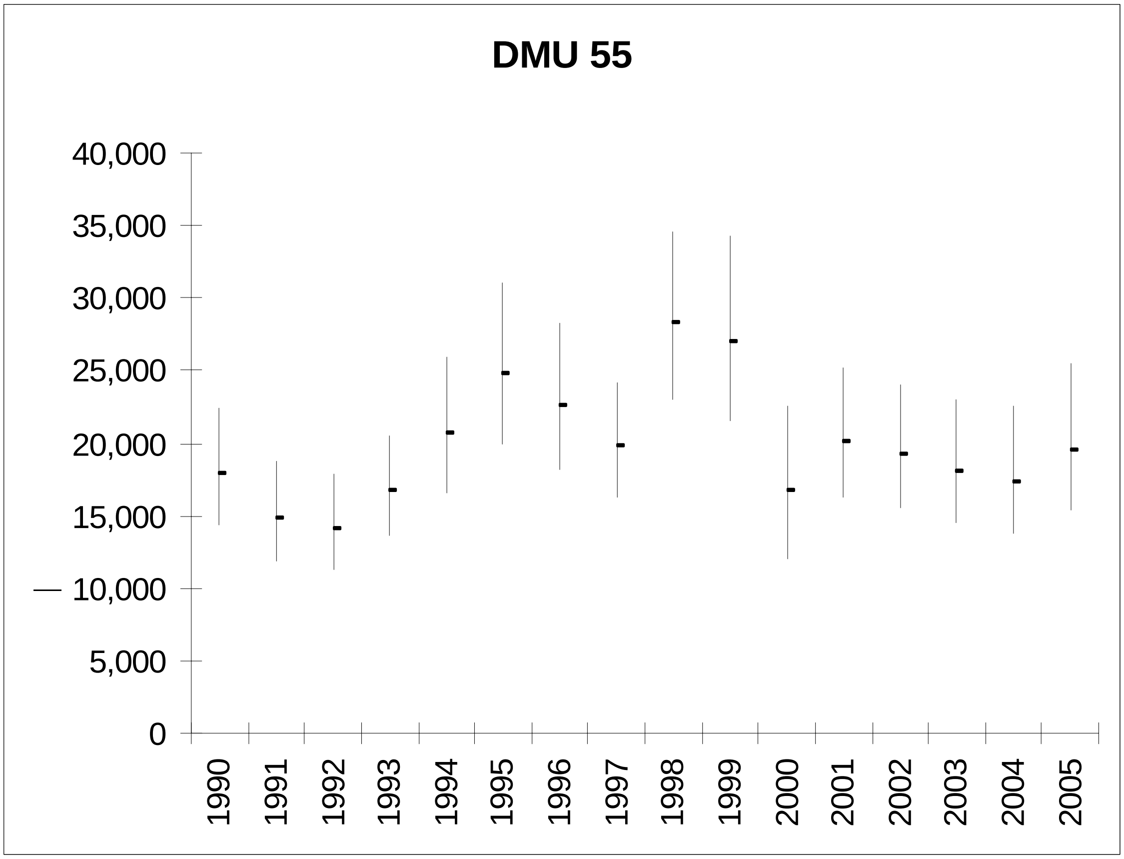


Figure 13. Population estimates and 90% confidence intervals, for the Wisconsin Sex-Age-Kill model, for white-tailed deer populations in Deer Management Units (DMU) 49B and 53, 1990–2005.



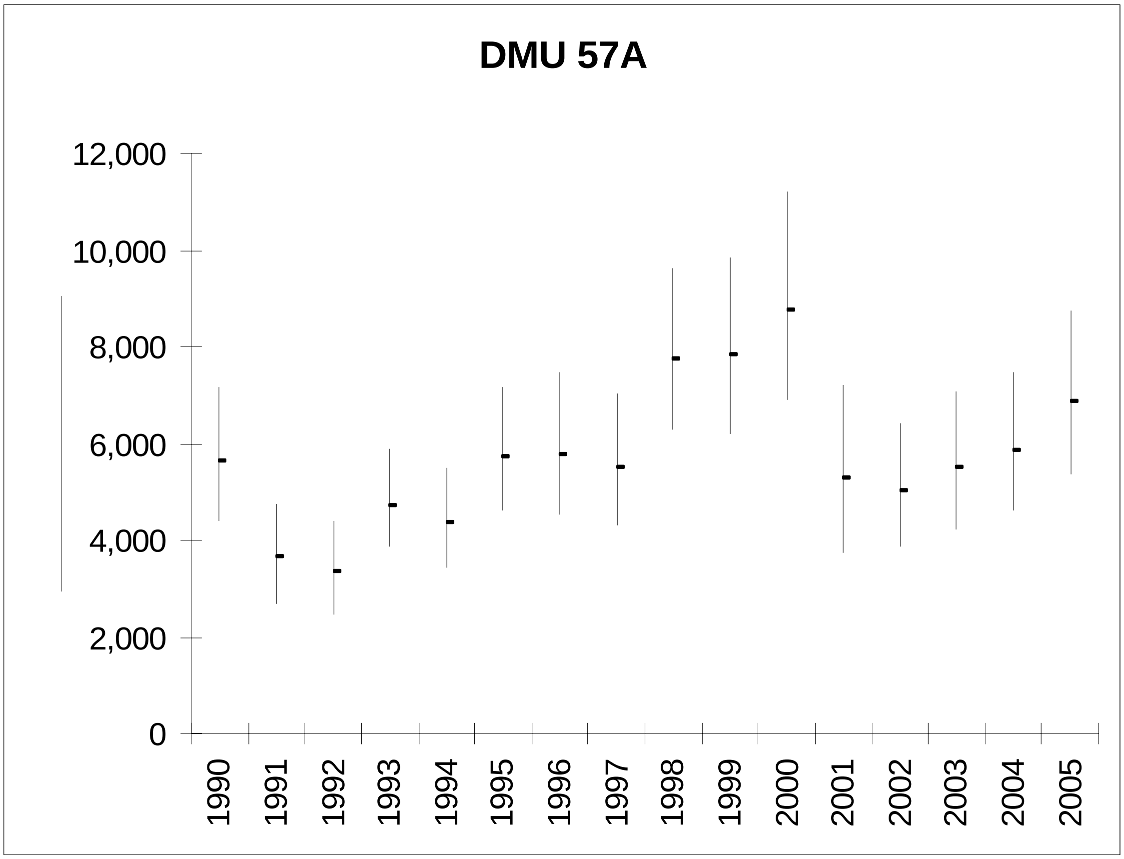


Figure 14. Population estimates and 90% confidence intervals, for the Wisconsin Sex-Age-Kill model, for white-tailed deer populations in Deer Management Units (DMU) 55 and 57A, 1990–2005.

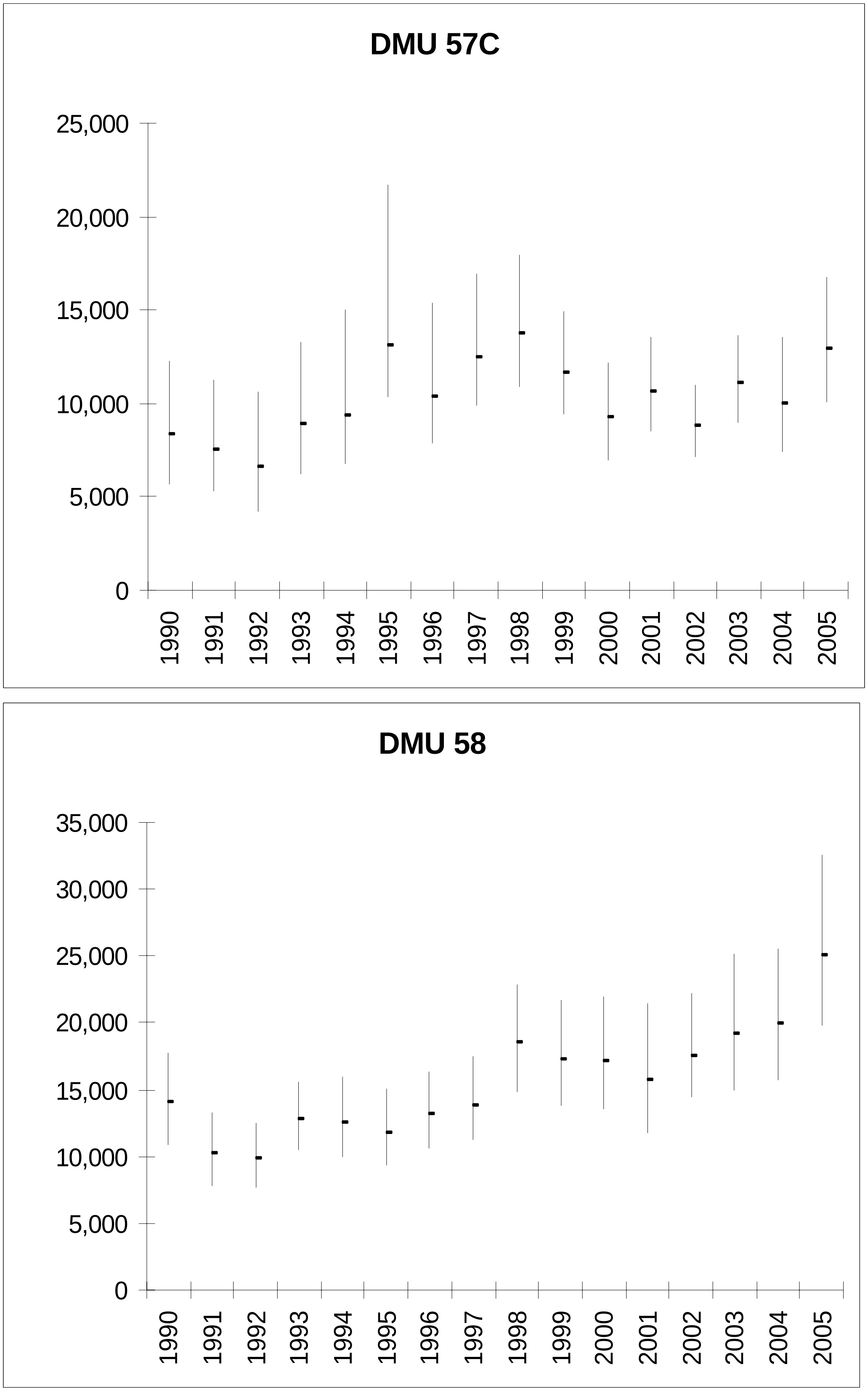


Figure 15. Population estimates and 90% confidence intervals, for the Wisconsin Sex-Age-Kill model, for white-tailed deer populations in Deer Management Units (DMU) 57C and 58, 1990-2005.

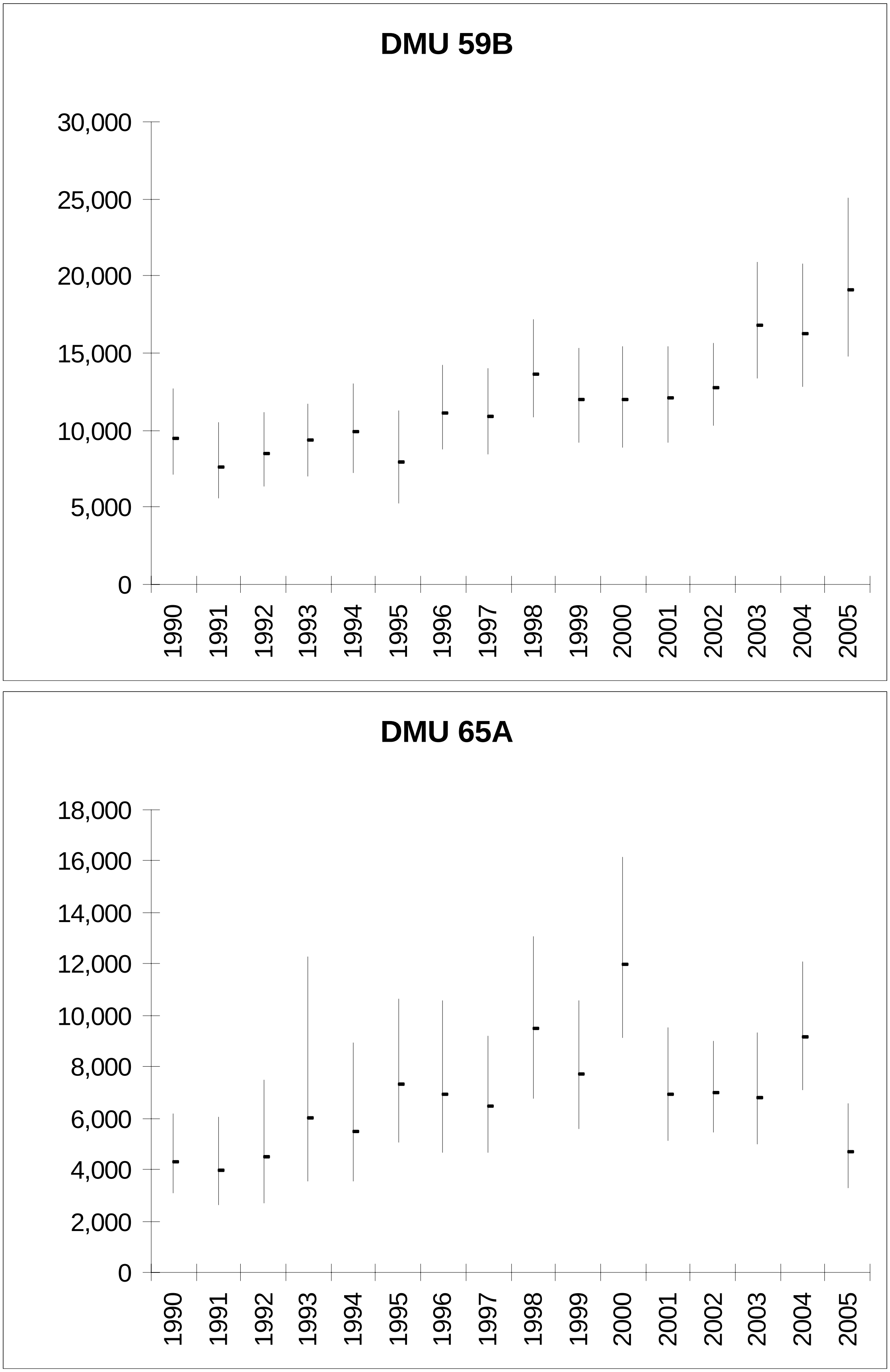


Figure 16. Population estimates and 90% confidence intervals, for the Wisconsin Sex-Age-Kill model, for white-tailed deer in Deer Management Units (DMU) 59B and 65A, 1990–2005.

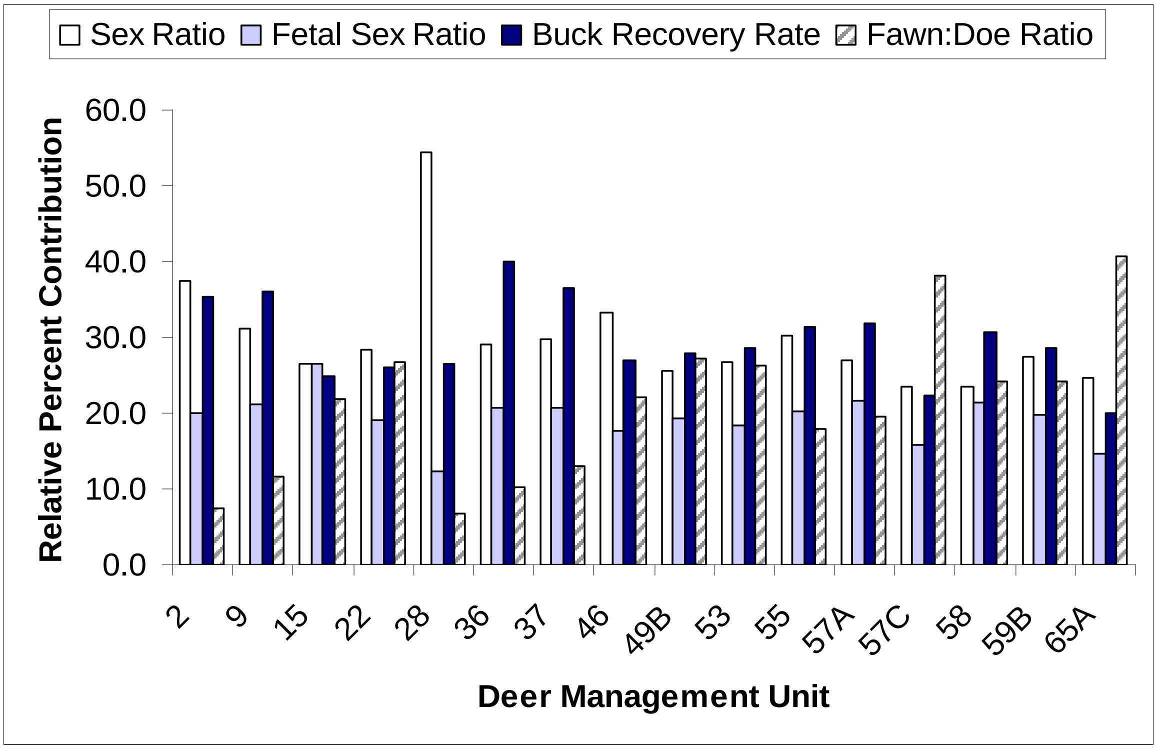
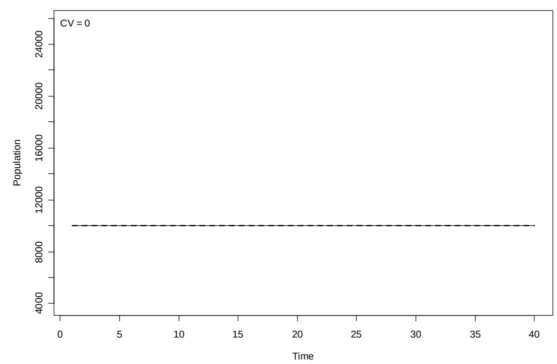
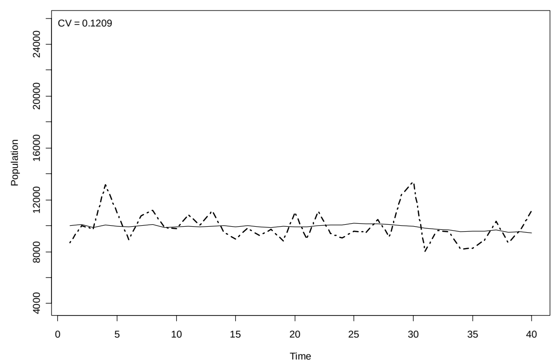


Figure 17. Relative contribution of each variable to the overall variability to population estimates of Deer Management Units (averaged over all years of data; 1990-2005; except DMU 49B, 1994-2005) in Wisconsin using the Sex-Age-Kill model. By allowing only one variable at a time to vary in the Monte Carlo simulation a measure of the contribution of each variable was obtained by expressing the proportion of CV from each variable to the sum of CVs for all variables.

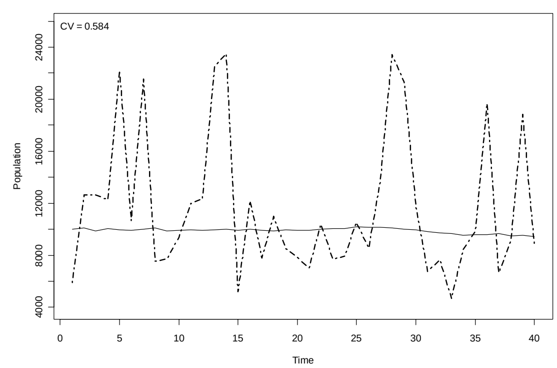
a. Deterministic model



b. Stochastic harvest and survival



c. Stochastic harvest sampling



d. Stochastic buck recovery rate

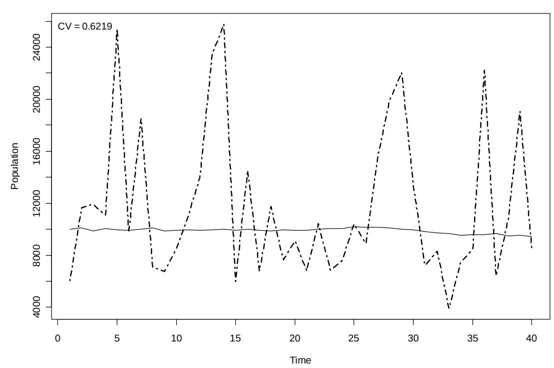
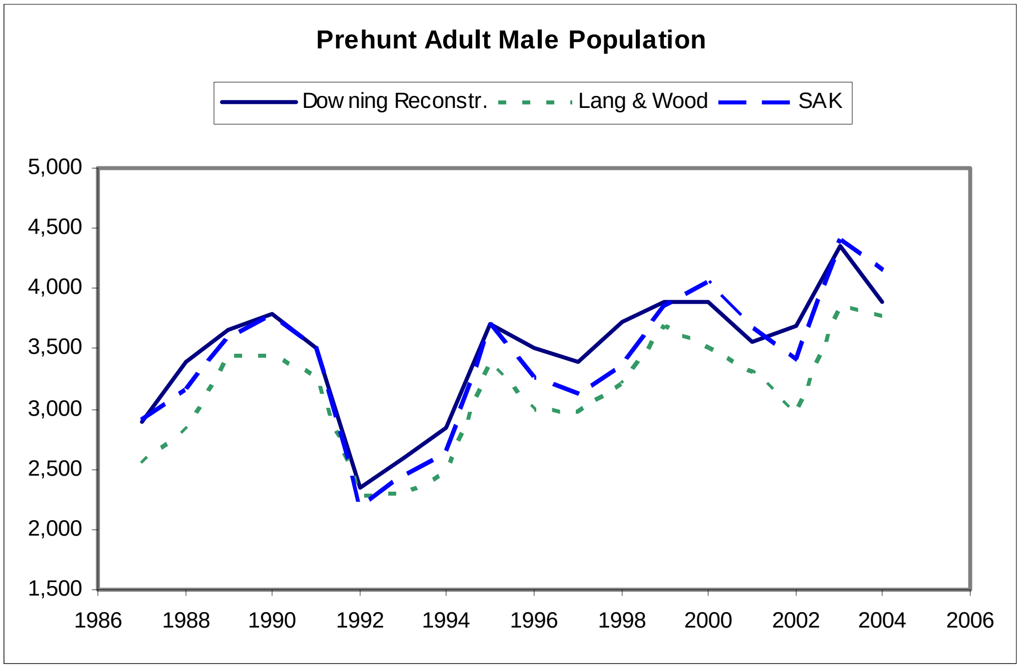


Figure 18. Illustration of population trends and corresponding SAK model estimates of abundance, N_i, under (a) deterministic stable-stationary conditions; (b) stochastic conditions; (c) stochastic variation and sampling error for p_{YM}, p_{YF}, and $R_{J/F}$; and (d) stochastic variation and sampling error for p_{YM}, p_{YF}, $R_{J/F}$, and B $(\theta = 1)$. Abundance from projection matrix model (solid line ———) and SAK estimates (dotted line - - - - - -).



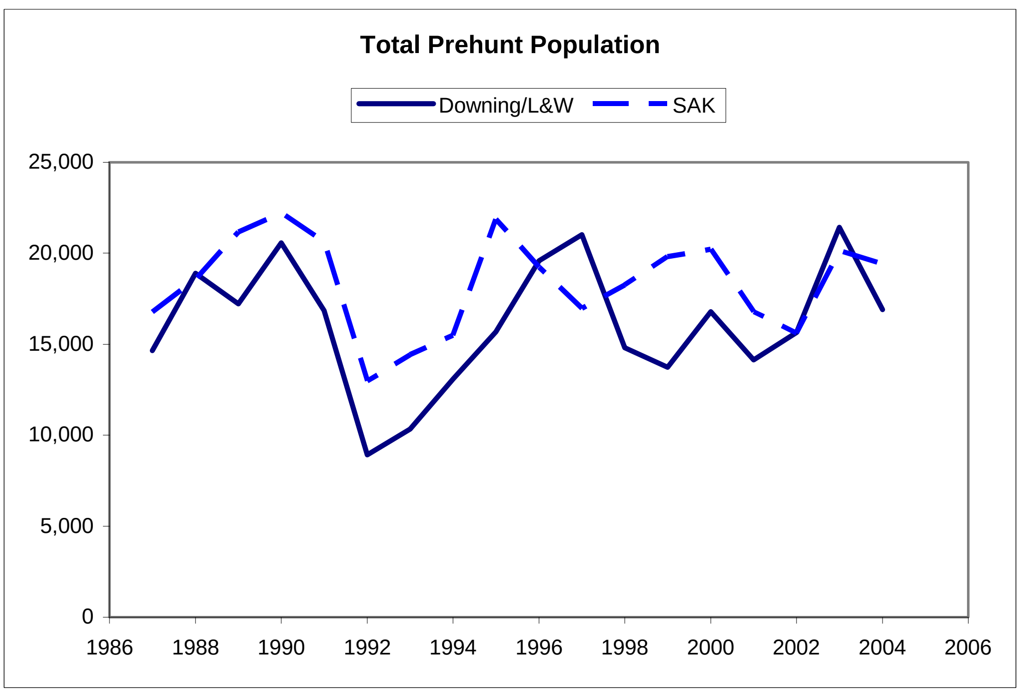
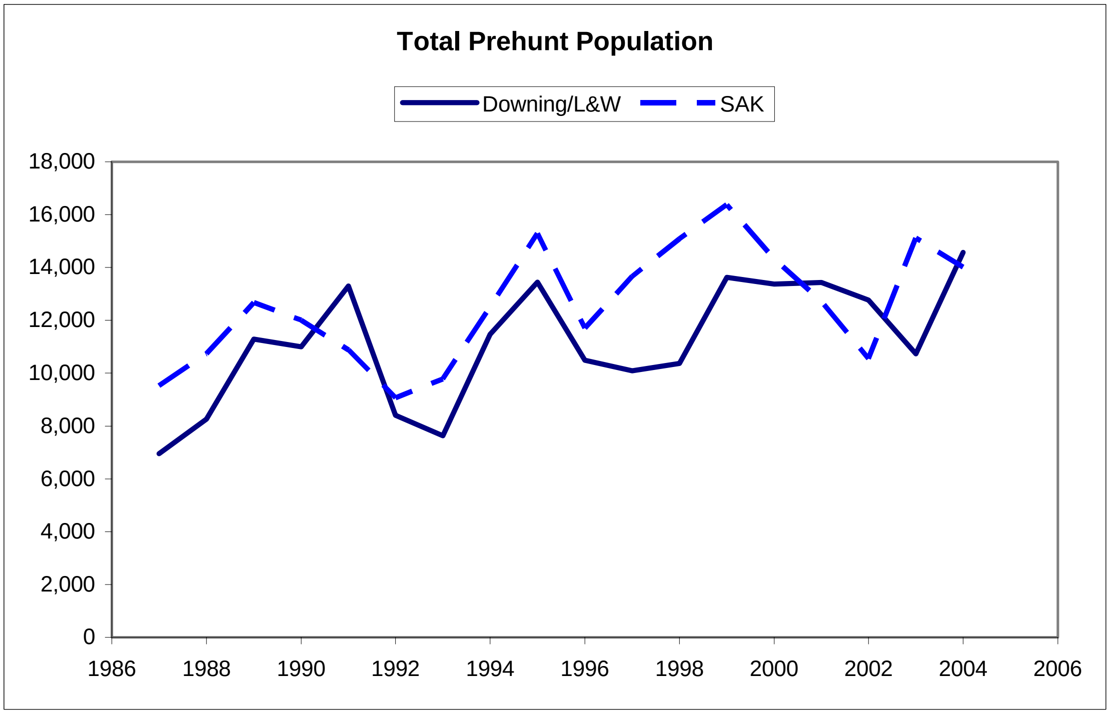


Figure 19. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 15 from 1986-2004 for prehunt adult male population (top) and total prehunt population (bottom).



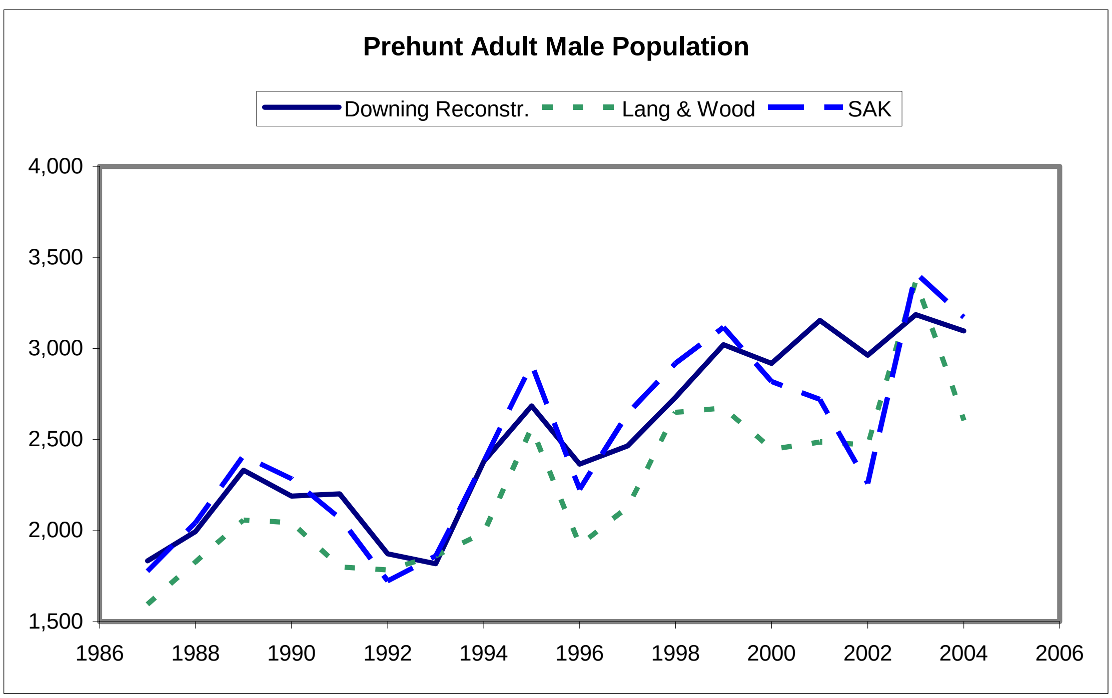
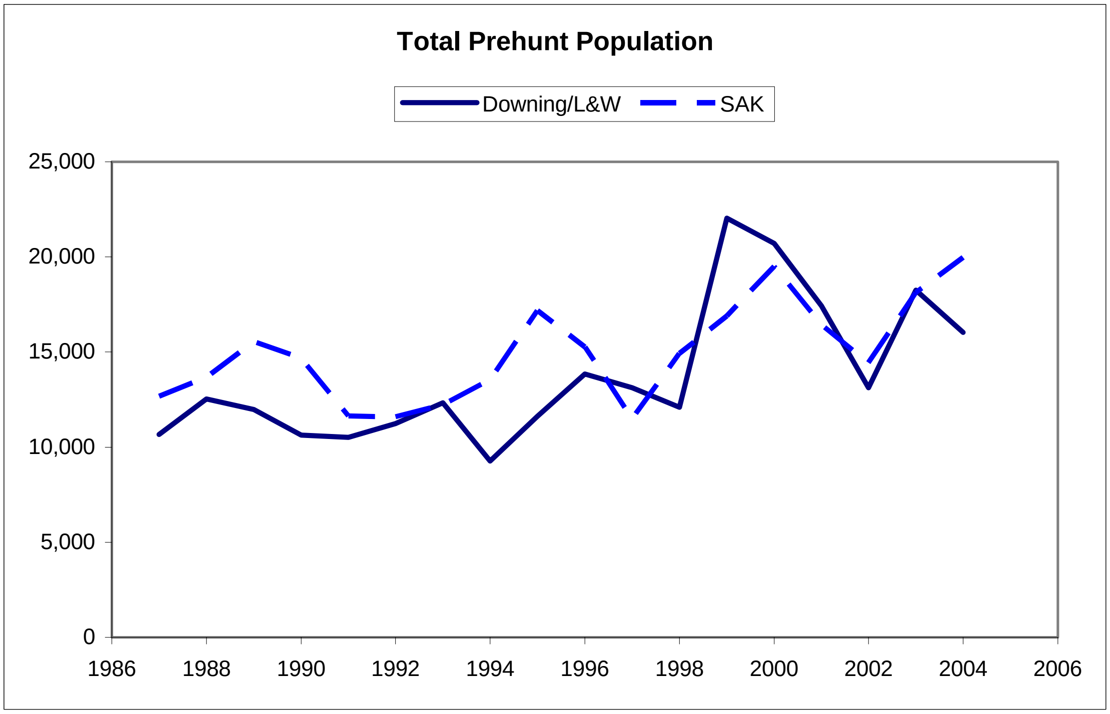


Figure 20. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 22 from 1986-2004 for total prehunt population (top) and prehunt adult male population (bottom).



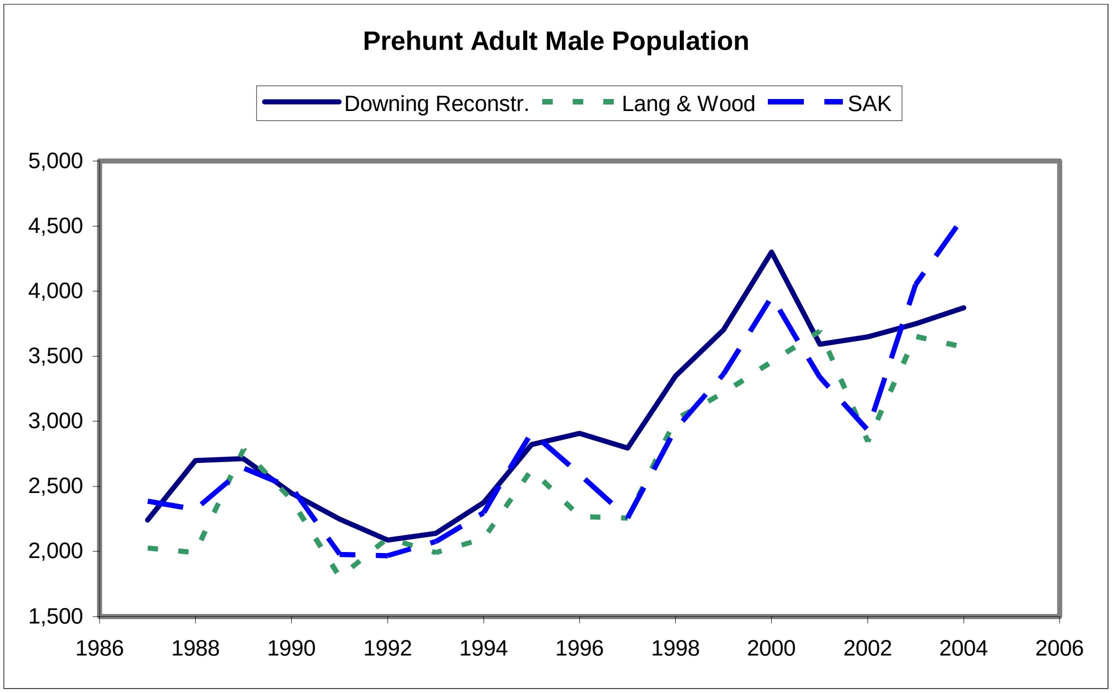
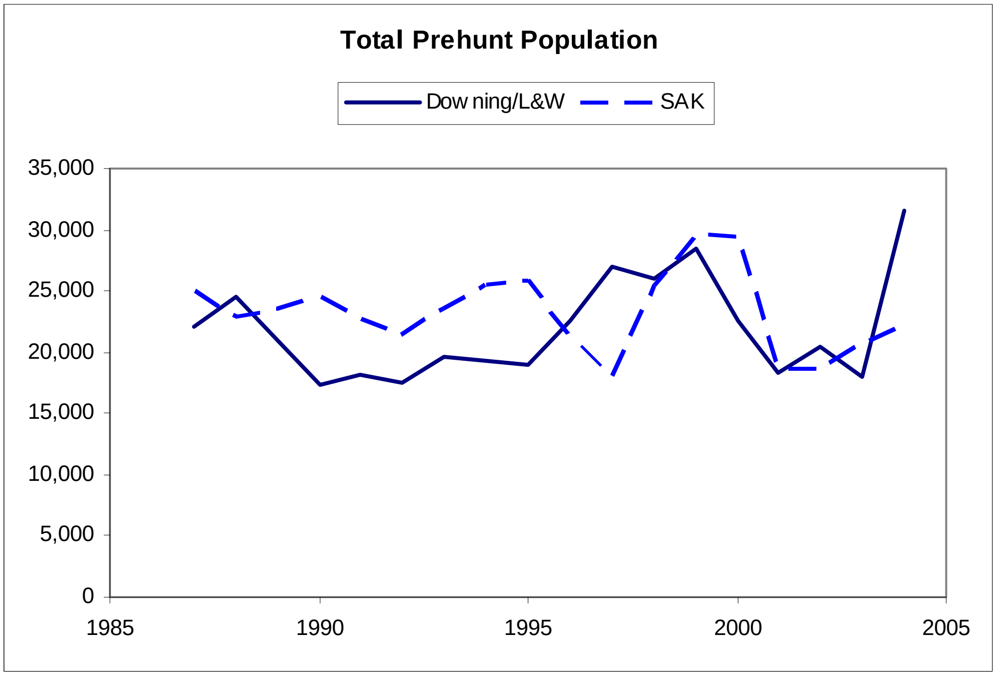


Figure 21. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 46 from 1986-2004 for total prehunt population (top) and prehunt male population (bottom).



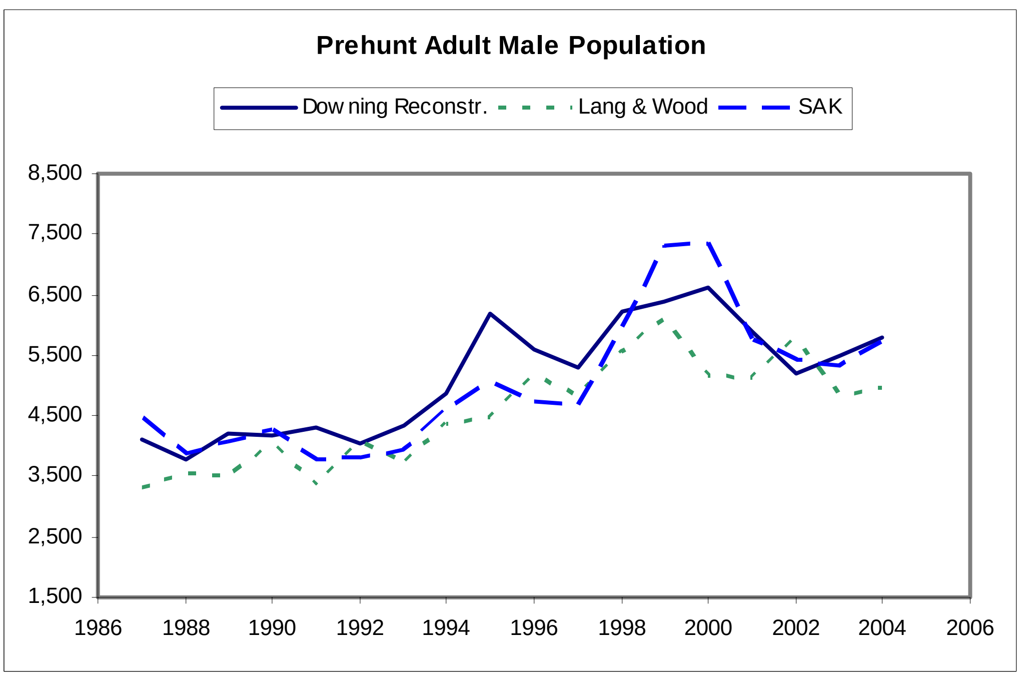
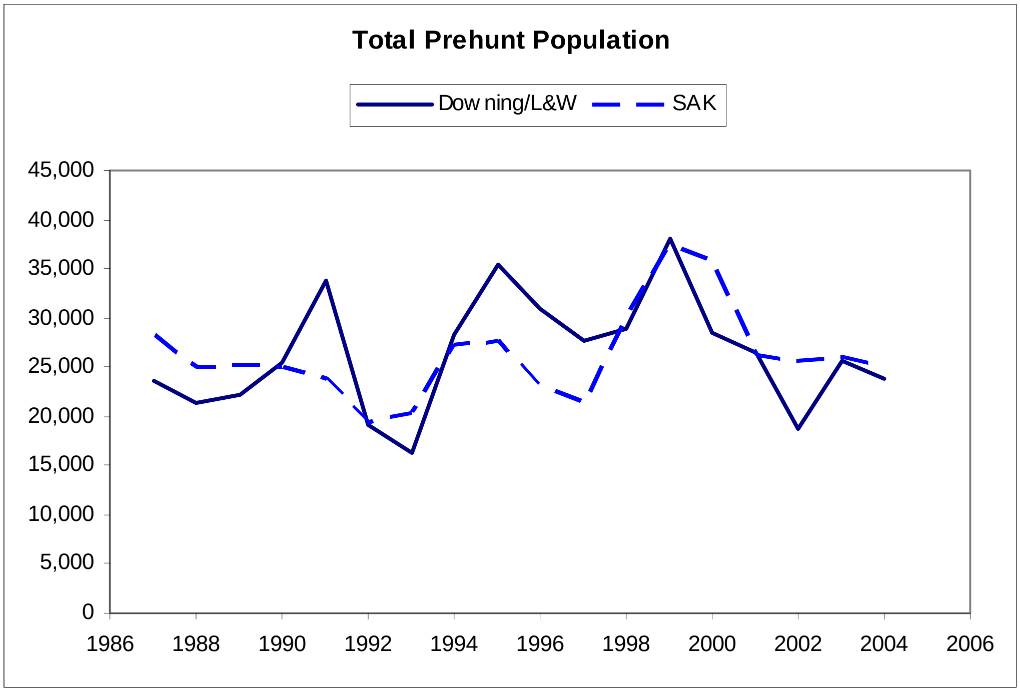


Figure 22. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 53 from 1986-2004 for total prehunt population (top) and prehunt male population (bottom).



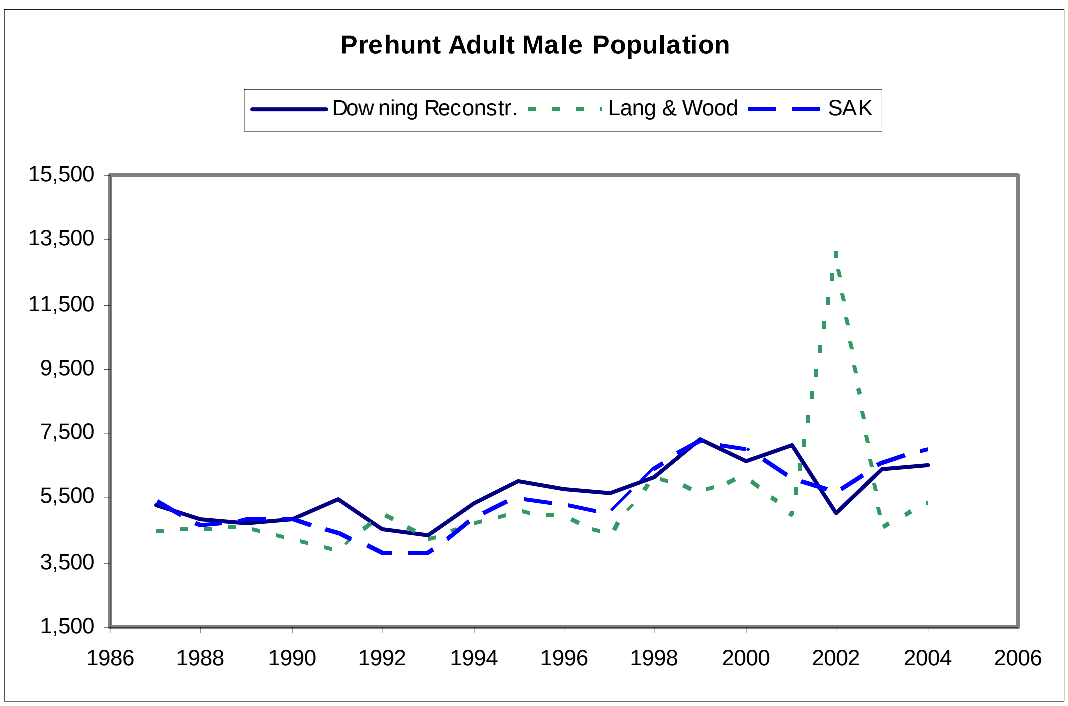
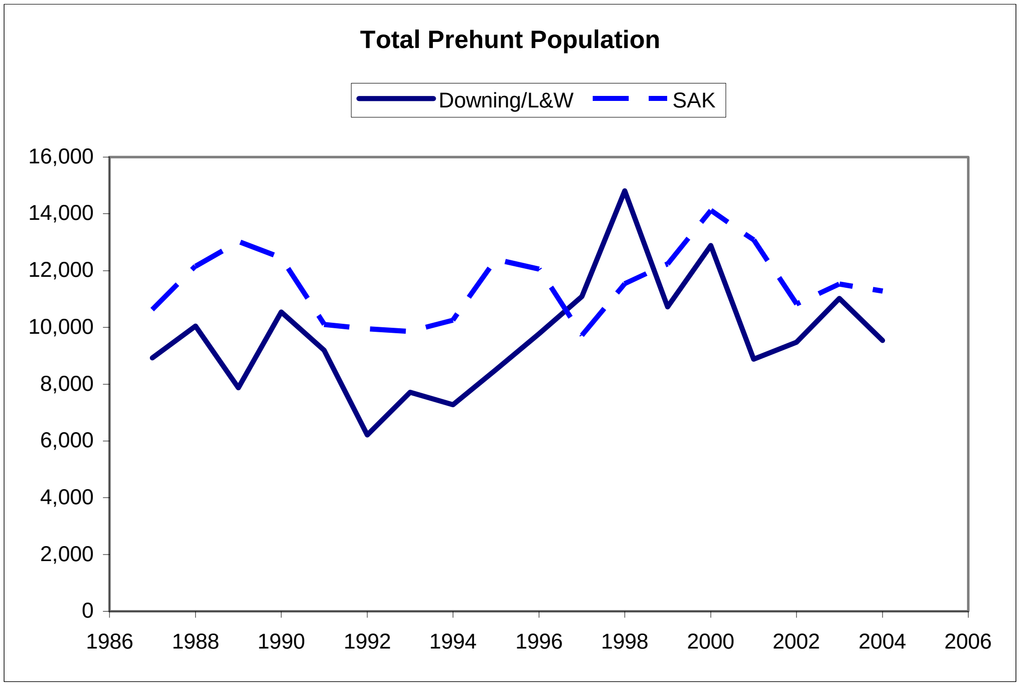


Figure 23. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 55 from 1986-2004 for total prehunt population (top) and prehunt male population (bottom).



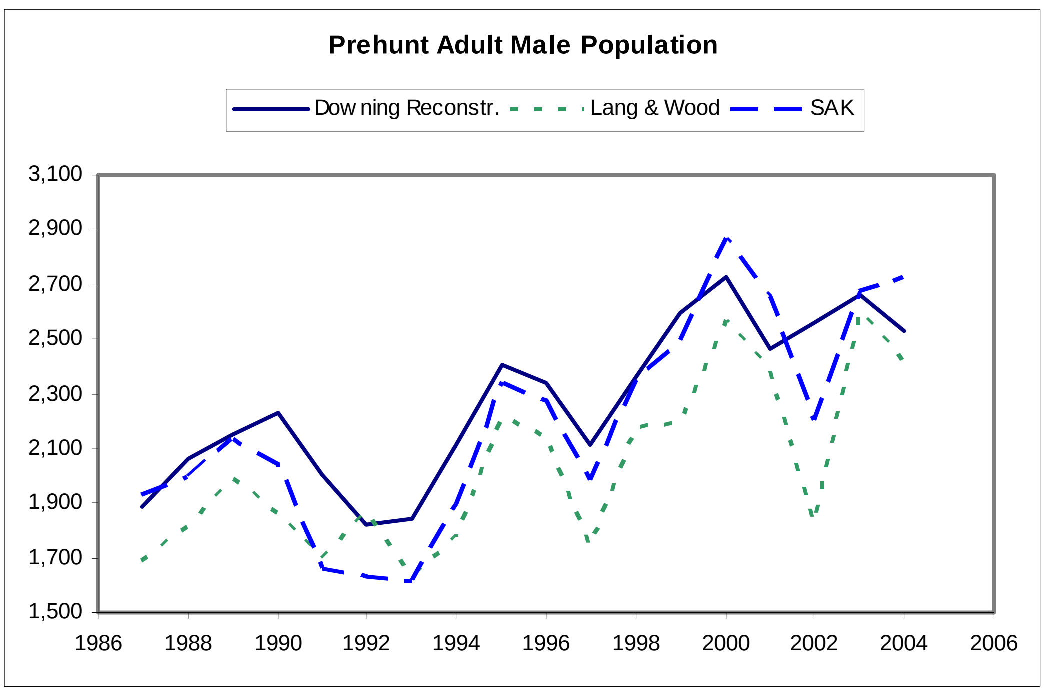
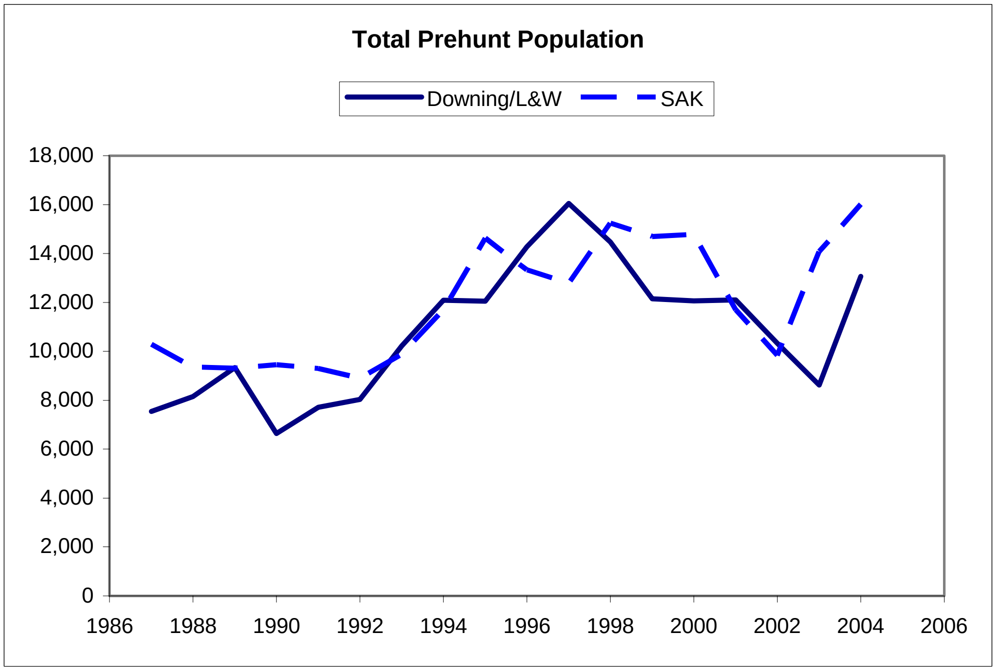


Figure 24. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 57A from 1986-2004 for total prehunt population (top) and prehunt male population (bottom).



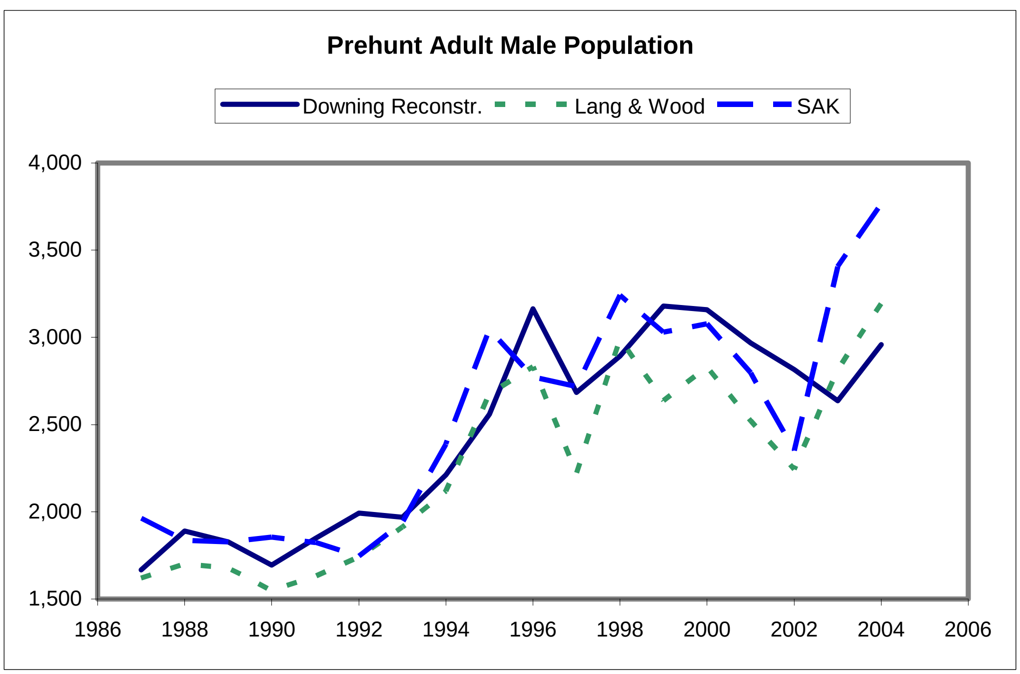
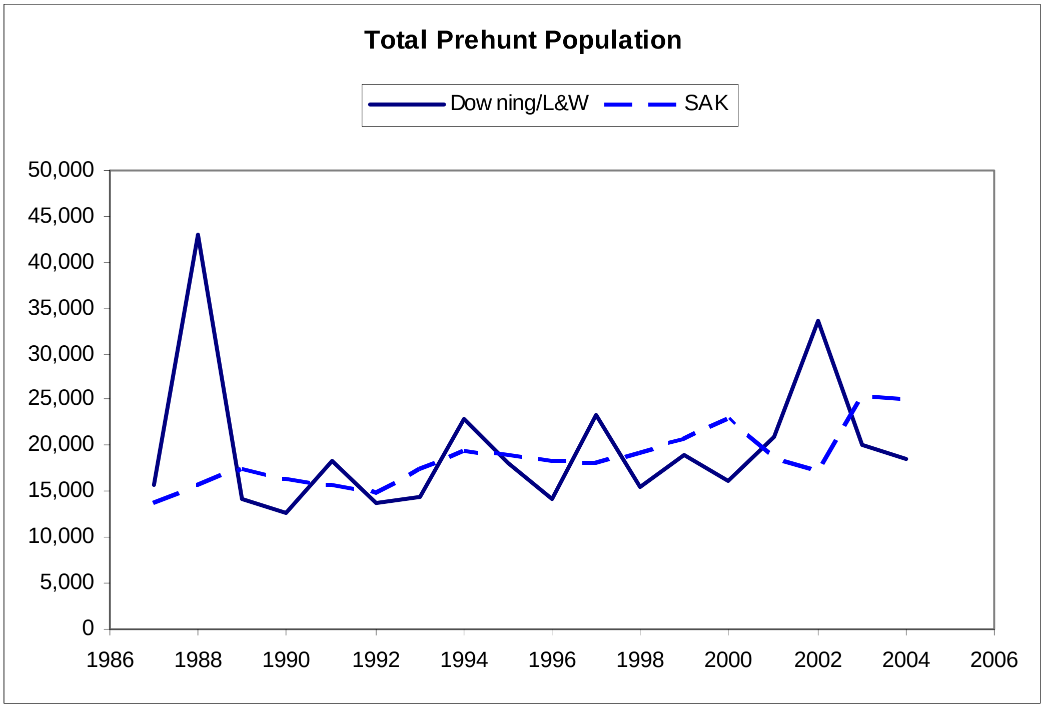


Figure 25. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 57C from 1986-2004 for total prehunt population (top) and prehunt male population (bottom).



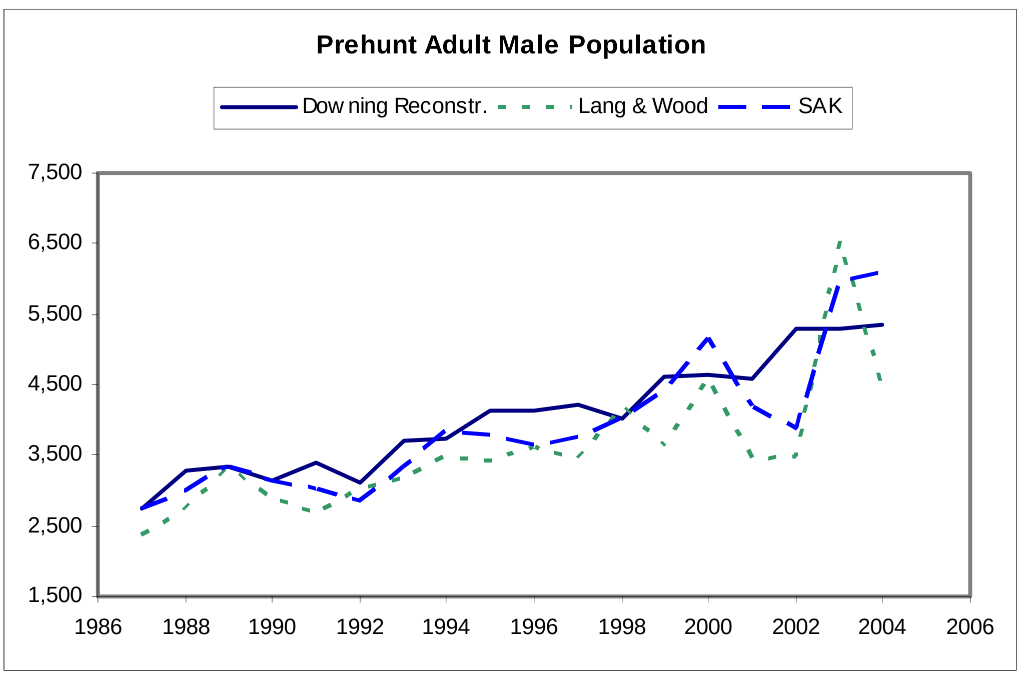
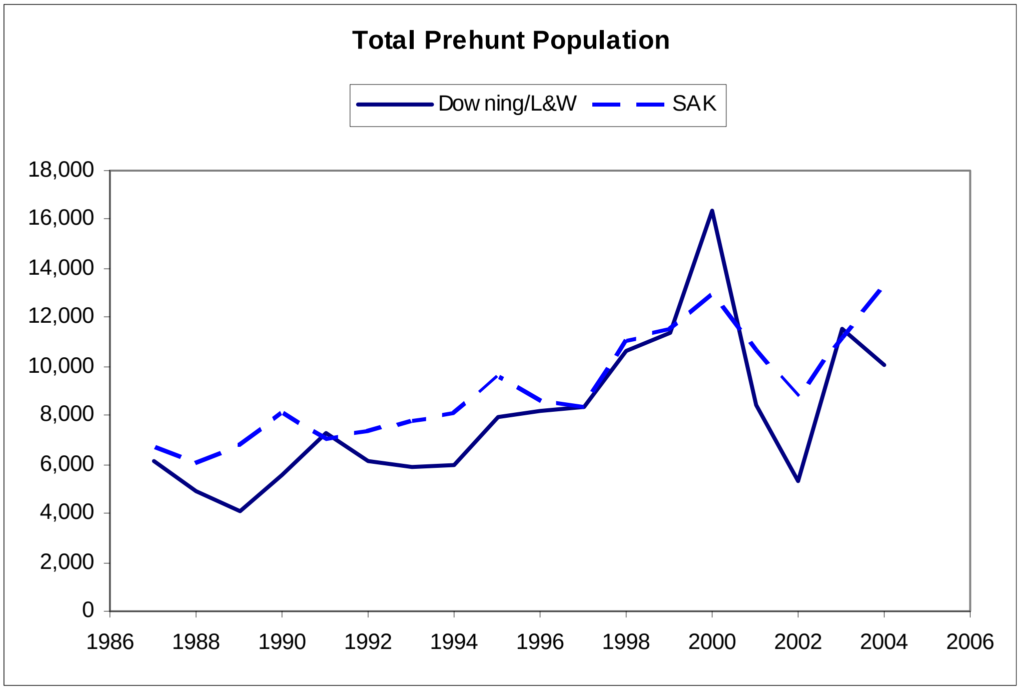


Figure 26. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 59B from 1986-2004 for total prehunt population (top) and prehunt male population (bottom).



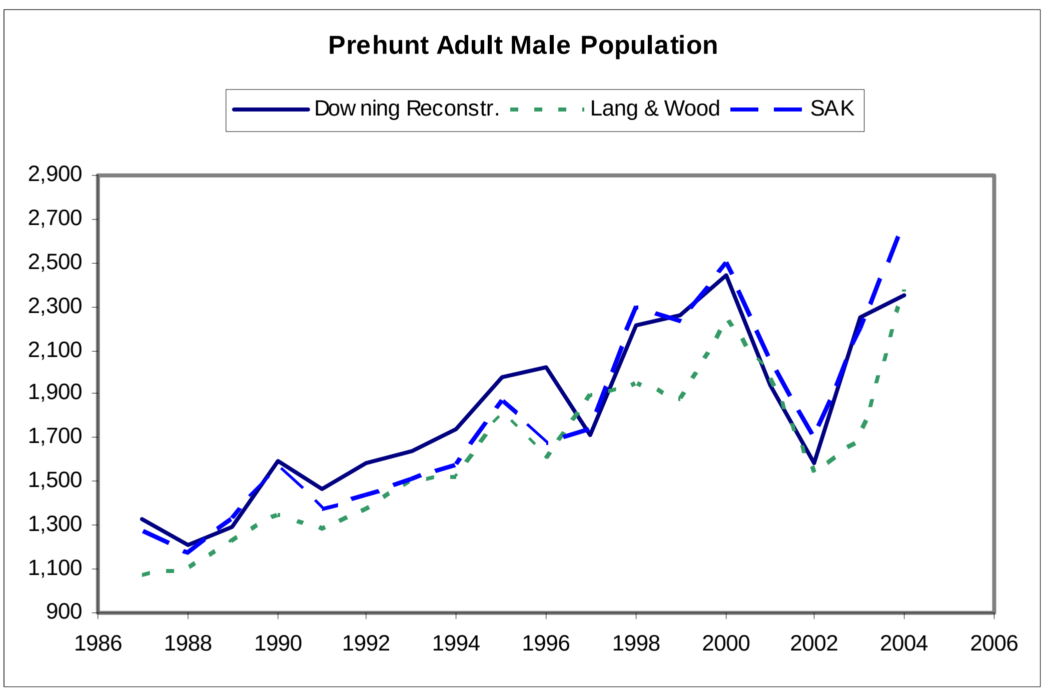


Figure 27. Comparison of Downing (1980), Lang and Wood (1976), and SAK population estimates for DMU 65A from 1986-2004 for total prehunt population (top) and prehunt male population (bottom).

Appendix A: Widespread and unit specific adjustments made to the SAK by WDNR personnel and their justification.

The WDNR occasionally makes unit-specific or wider adjustments to $\hat{B}$ and fawn:doe ratios. Adjustments to $\hat{B}$ are conditional on weather conditions before and during the hunt, hunter pressure, and other factors. Adjustments to fawn:doe ratios have occurred due to an uneven distribution of observations in July. Below we document the adjustments and their justification.

2002

The November 2002 firearm season opened on the latest possible date. Hunter access was good because back roads and wetlands were frozen. Temperatures during the season were colder than normal and high winds occurred during the opening weekend and later in the week. Snow cover was lacking throughout the season in most of the state. Parts of the north received snow early in the week and again at the end of the season.

Hunting pressure appeared to be affected by the discovery of chronic wasting disease in southwestern Wisconsin earlier in the year. Sales of gun and archery deer licenses were lower than in 2001 by 10% and 19%, respectively. Estimates of hunter pressure during the opening weekend of the November gun season were 13% lower then in 2001. *Consequently, the Deer Committee decided to lower the estimates of buck recovery rate for Northern Forest units by 5-11%.* This lowered the estimate of buck harvest rate by an average of 7% across the region and increased the estimated prehunt 2003 population in the Northern Forest by 7%. Adjustments in buck recovery rates were not believed to be necessary in other regions because recorded buck harvests were less depressed than in the Northern Forest.

1998

Hunting conditions during the November 1998 gun season were considered to be better than normal. Corn harvest progress was well ahead of the 5-year average. Much of the Northern Forest had light snow cover for opening weekend. Temperatures were generally above normal after opening day. There was no significant precipitation during the season. *Based on the good hunting conditions, the Deer Advisory Committee decided to increase the estimates of buck recovery rates used in the SAK formula for Northern Forest Units.*

1996

For forested management units, the fawn:doe ratios used in the SAK formula have been based on the annual summer deer observation survey. In past years, observations from July, August, and September have been approximately equal in number and were pooled to calculate the fawn:doe ratio for groupings of management units. However, in 1996 the number of observations from July greatly exceeded the number of observations from August and September. Because the fawn:doe ratio of July observations is typically lower than the other two months, we felt that pooling of all observations would underestimate the true ratio. *Therefore, we used the average of the three monthly estimates of fawn:doe ratio in the SAK formula for the forested units.* As in past years, long-term estimates of fawn:doe ratios were used for farmland units, because of concern about the accuracy of the annual summer deer observations from these regions.

Unit specific adjustments

Below are unit specific adjustments made by DNR personnel.

1999

In 1999, adjustments were made in 9 DMUs. In three DMUs (62B, 65B, and 67B) *the buck recovery rate was adjusted downward because they had a Zone T season framework with an unlimited number of free antlerless permits*. It was believed that the availability of antlerless permits might have reduced buck harvest rates in these units. In several other southern farmland DMUs there was considerable debate over proposed updates to yearling buck and doe percents and buck recovery rates See "SW Non EAB Comments.doc" and "SW Farmland SAKs.xls".

1998

In 1998, adjustments were made in 4 DMUs (56, 67A, 76, and 76M). DMU 67A had a season framework equivalent to "Zone T" with an unlimited number of free antlerless permits. *DMUs 76 and 76M include and surround Madison and the local manager believed that limited hunter access and high numbers of traffic accidents warranted a lower buck recovery rate.*

1997

In 1997, adjustments were made in 8 DMUs (56, 61, 62B, 63B, 70, 74A, 76 and 76M). Five of the DMUs had a "Zone T" season framework with an unlimited number of free antlerless permits. *DMUs 76 and 76M include and surround Madison and the local manager believed that limited hunter access and high numbers of traffic accidents warranted a lower buck recovery rate.*

1994

In the 1994 SAK spreadsheet that was included with the 2/6/2006 message 9 farmland units were highlighted in green, indicating that adjusted buck recovery rates were used. These should be considered "updated" rather than "adjusted" because we were starting the process of updating yearling percent model inputs in recognition of the changes in yearling buck percents in the farmland region.

Appendix B: Simulation Models Used in SAK Evaluation

Deterministic Model

For all deterministic computer runs, a two-sex Leslie matrix model with harvest was used. These simulations included *no* stochastic variability in recruitment or survival. Annual abundance and harvest numbers are computed directly from matrix multiplication of a two-sex model,

$$\mathbf{M} \cdot \mathbf{H} \underset{\sim}{n}_i = \underset{\sim}{n}_{i+1},$$

where

$\mathbf{M}$ = Leslie two-sex model;

$\mathbf{H}$ = harvest matrix;

$\underset{\sim}{n}_i$ = vector of abundance by sex and age in year i;

and where

$$\left[\begin{array}{cccc|cccc}
F_{0F} & F_{1F} & \dots & F_{iF} & & & & \\
S_{0F} & 0 & & & & & & \\
0 & S_{1F} & & & & & & \\
 & & S_{AF} & 0 & & & & \\
\hline
F_{0M} & F_{1M} & \dots & F_{AM} & 0 & 0 & \dots & 0 \\
 & & & & S_{0M} & 0 & \dots & 0 \\
 & & 0 & & 0 & S_{1M} & & \\
 & & & & & & S_{AM} & 0
\end{array}\right]$$

$$\cdot \begin{bmatrix} h_{0F} & & & & & & & \\ & h_{1F} & & & & & & \\ & & \ddots & & & & & \\ & & & h_{AF} & & & & \\ & & & & h_{0M} & & & \\ & & & & & h_{1M} & & \\ & & & & & & \ddots & \\ & & & & & & & h_{AM} \end{bmatrix} \cdot \begin{bmatrix} n_{0Fi} \\ n_{1Fi} \\ \vdots \\ n_{AFi} \\ n_{0Mi} \\ n_{1Mi} \\ \vdots \\ n_{AMi} \end{bmatrix} = \begin{bmatrix} n_{0F,i+1} \\ n_{1F,i+1} \\ \\ n_{AF,i+1} \\ n_{0M,i+1} \\ \vdots \\ \\ m_{AM,i+1} \end{bmatrix},$$

and where

F_{iF} = net number of female offspring recruited per female of age $i\ (i = 0,\ldots,A)$ into the fall huntable population;

F_{iM} = net number of male offspring recruited per female of age $i\ (i = 0,\ldots,A)$ into the fall huntable population;

S_{iM} = probability of annual survival from natural causes for a female of age i to $i+1$ $(i = 0,\ldots,A)$ from fall to fall;

S_{iM} = probability of annual survival from natural causes for a male of age i to $i+1$ $(i = 0,\ldots,A)$ from fall to fall;

h_{iF} = probability of surviving harvest for a female of age $i\ (i = 1,\ldots,A)$;

h_{iM} = probability of surviving harvest for a male of age $i\ (i = 1,\ldots,A)$;

n_{jFi} = number of females of age class j in year $i\ (j = D,\ldots,A)$ in the fall huntable population;

n_{jMi} = number of males of age class j in year $i\ (j = D,\ldots,A)$ in the fall huntable population.

Multiply through; then

$$\begin{bmatrix} n_{0F,i+1} \\ n_{1F,i+1} \\ \vdots \\ n_{AF,i+1} \\ n_{0M,i+1} \\ n_{1M,i+1} \\ \vdots \\ n_{AM,i+1} \end{bmatrix} = \begin{bmatrix} \sum_{j=0}^{A} n_{jFi} \cdot F_{jF} \cdot h_{jF} \\ n_{0Fi} S_{0F} h_{0F} \\ \vdots \\ n_{A-1,F,i}, S_{A-1,F} h_{A-1,F} \\ \sum_{j=0}^{A} n_{jFi} \cdot F_{jM} \cdot h_{jF} \\ n_{0Mi} S_{0M} h_{0M} \\ \vdots \\ n_{A-1,M,i} S_{A-1,M}\, j_{A-1,M} \end{bmatrix}. \tag{B1}$$

In the simulation runs, age classes 0.5, 1.5, . . . ,12.5 were modeled. Successive generations of deer were simulated by recursively using Eq. (A1). Annual harvest $\left(\underset{\sim}{c}_i\right)$ of deer by age and sex class was calculated as the vector

$$\underset{\sim}{c} = (\mathbf{I} - \mathbf{H})\mathbf{M}\underset{\sim}{\mathbf{n}}_{\mathbf{i}}\,. \tag{B2}$$

Total annual harvest $\left(TH_i\right)$ was calculated as

$$TH_i = \underset{\sim}{\mathbf{1}}'(\mathbf{I} - \mathbf{H})\mathbf{M}\underset{\sim}{\mathbf{n}}_{\mathbf{i}} = \underset{\sim}{\mathbf{1}}'\underset{\sim}{\mathbf{c}}\,. \tag{B3}$$

Stochastic Model

The stochastic versions of model A1 was based on binomial sampling for the natural survival and harvest processes and a Poisson recruitment function. The harvest for a particular age and sex class was modeled as a binomial process, where

$$c_{ij} \sim \mathrm{BIN}\left(n_{ij}, \left(1 - h_{ij}\right)\right), \tag{B4}$$

where

c_{ij} = harvest for age class i, gender j;

n_{ij} = abundance for age class i, gender j;

h_{ij} = probability of surviving harvest age for class i, gender j.

Next year's abundance was then modeled as a binomial process conditional on c_{ij}, where

$$n_{i+1,j} \sim \mathrm{BIN}\left(n_{ij} - c_{ij}, S_{ij}\right), \tag{B5}$$

where S_{ij} = probability of surviving natural causes for age class i, gender j. Recruitment of age class 0.5 was based on the expected values in Eq. (A1), where

$$E\left(n_{0j}\right) = \sum_{j=0}^{A}\left(n_{iF} - c_{iF}\right)F_{ij} = \mu_{0j},$$

where

F_{ij} = fecundity of age class i in producing gender j offspring;

n_{iF} = number of age class i females,

c_{iF} = number of age class i females harvested.

The number of 0.5 age class individuals in the population was then treated as a Poisson random variable, where

$$n_{0j} \sim \mathrm{Poisson}\left(\mu_{0j}\right). \tag{B6}$$

Appendix C. Computer program (SAS code) used to estimate the precision of Wisconsin SAK population estimates for white-tailed deer.

```
****************************************************************
*
* Program to estimate precision of WI's SAK deer model.
*
*    Input Variables:
*    yr   = year data collected
*    dmu  = deer mgt unit
*    area = size of DMU in sq. miles
*    bkill = no. legal bucks killed
*    cbuck = no. antlered deer aged
*    p18 - p54 = percent of buck kill by age class (months)
*    dkill = no. antlerless deer killed
*    cdoe = no. antlerless deer aged
*    p6m, p18m = percent of antlerless kill by sex (males) and age class (months)
*    p6f - p54f = percent of antlerless kill by sex (females) and age class
(months)
*    fsight = no. fawns sighted
*    dsight = no. adult females sighted
*    fdratio = fawn:doe ratio
*    region = mgt region
*    group = DMU group
*
*    Calculated Variables:
*    cm18 = no. 18 mo old bucks aged
*    f18 = no. 18 mo old females aged
*    ad_doe = no. 18+ mo old females aged
*    yb = proportion of yearling bucks in harvest (5-yr running average)
*    yd = proportion of yearling does of all adult does in harvest (5-yr running
avg)
*    birthratio = male:female fetal ratio
*    adsxratio = male:female adult ratio
*    brr = buck recovery rate as a function of yb
*    bhr = buck harvest rate (yb*brr/100)
*    buckpop = preseason buck abundance
*    doepop = preseason doe abundance
*    fdratio = fawn:doe ratio (5-yr running average)
*    fawnpop = preseason fawn abundance
*    prehuntpop = preseason total deer abundance
*    prehuntdens = preaseason total deer density
*    loss = crippling loss and unreported harvest
*    posthuntpop = postseason total deer abundance
*    posthuntdens = postseason total deer density
*
* Written by Duane R. Diefenbach, May 2006
********************************************************************************
*****;

**************************************
*********************Import data;
PROC IMPORT OUT=agedeer
       DATAFILE= "E:\My Documents\Deer research\Wisconsin\Input for selected
DMUs.xls"
            DBMS=EXCEL2000 REPLACE;
```

```
     GETNAMES=YES;
proc sort; by dmu1 dmu2 yr;
RUN;

*************************************************
***********Calculate population point estimates;
data one; set agedeer;
dmu=compress(dmu1||dmu2);

*****Yearling Buck and Doe Percentages;
 cm18=round(p18*cbuck); f18=round(p18f*cdoe);
ad_doe=round((p18f+p30f+p42f+p54f)*cdoe);
 if f18=. then do; f18=0; ad_doe=0; end;
 if cm18=. then do; cm18=0; cbuck=0; end;
      yb=(cm18+lag1(cm18)+lag2(cm18)+lag3(cm18)+lag4(cm18))/
         (cbuck+lag1(cbuck)+lag2(cbuck)+lag3(cbuck)+lag4(cbuck));
      yd=(f18+lag1(f18)+lag2(f18)+lag3(f18)+lag4(f18))/
         (ad_doe+lag1(ad_doe)+lag2(ad_doe)+lag3(ad_doe)+lag4(ad_doe));
 if lag4(dmu)^=dmu then yd=.;

*****Adult sex ratio and buck harvest rate;
 birthratio=1.0892;
 adsxratio=(yb/yd)/birthratio;
 brr=(96.7)*(1-exp(-.051*(yb*100-31)));
 bhr=yb*brr/100;

*****Adult male and female population;
 buckpop=bkill/bhr; doepop=buckpop*adsxratio;

*****Fawn:doe ratio and fawn population;
 fdratio=(fsight+lag1(fsight)+lag2(fsight)+lag3(fsight)+lag4(fsight))/
         (dsight+lag1(dsight)+lag2(dsight)+lag3(dsight)+lag4(dsight));
 fawnpop=doepop*fdratio;

*****Final population estimates;
 prehuntpop=buckpop+doepop+fawnpop;
 prehuntdens=prehuntpop/area;
 loss=(bkill+dkill)*.15;
 posthuntpop=prehuntpop-bkill-dkill-loss;
 posthuntdens=posthuntpop/area;

proc sort; by dmu1 dmu2 yr;

proc print label noprint;
 label yr='Year' dmu='DMU' bkill='Antlered harvest' dkill='Antlerless harvest'
       yb='harv rate 18 male' buckpop='Buck population'
       fawnpop='Fawn population' doepop='Adult female population'
       fdratio='fawn:adultf ratio' prehuntpop='Preseason Population Size’
       prehuntdens='Preseason population density'
       posthuntpop='Postseason Population Size'
       posthuntdens='Postseason population density'
       cbuck='No. bucks aged';
 format bkill cm18 dkill f18 buckpop doepop fawnpop prehuntpop comma6.0
        p18 p18f fdratio adsxratio yb yd 6.3;
 var yr dmu bkill p18 cbuck yb dkill p18f cdoe yd adsxratio
     buckpop doepop fawnpop posthuntpop posthuntdens;
```

```
***********************Monte Carlo estimation of
CI******************************
rep=# bootstrap replicates;

%let rep=999;  *number of bootstraps;
%let one=999; %let two=1998; %let three=2997; %let four=3996;
data five; set one;
 *****Random Seeds for CALL statements;
 seed1=int(ranuni(0)*10**7); seed2=int(ranuni(0)*10**7);
seed3=int(ranuni(0)*10**7);
 seed4=int(ranuni(0)*10**7); seed5=int(ranuni(0)*10**7);
 seed6=int(ranuni(0)*10**7); seed7=int(ranuni(0)*10**7);

do i=1 to &rep;
*****Yearling Buck and Doe Percentages;
 call ranbin(seed1,cbuck,p18,xbin1);
 ad_doe=round(cdoe*(p18f+p30f+p42f+p54f)); pdoe=p18f/(p18f+p30f+p42f+p54f);
 call ranbin(seed2,ad_doe,pdoe,xbin2);
 cm18=xbin1; f18=xbin2;
 if f18=. then do; f18=0; ad_doe=0; end;
 if cm18=. then do; cm18=0; cbuck=0; end;
      yb=(cm18+lag&one(cm18)+lag&two(cm18)+lag&three(cm18)+lag&four(cm18))/
         (cbuck+lag&one(cbuck)+lag&two(cbuck)+lag&three(cbuck)+lag&four(cbuck));
      yd=(f18+lag&one(f18)+lag&two(f18)+lag&three(f18)+lag&four(f18))/

(ad_doe+lag&one(ad_doe)+lag&two(ad_doe)+lag&three(ad_doe)+lag&four(ad_doe));
 if lag&four(dmu)^=dmu then yd=.;

*****Fawn Sex Ratio and Adult Sex Ratio;
 call ranbin(seed3,1803,940/1803,xbin3);
 males=xbin3;
 birthratio=males/(1803-males);
 adsxratio=(yb/yd)/birthratio;

*****Buck Recovery and Harvest Rates and Adult Male/Female Population Size;
 cv=.05; *arbitrary precision of BRR parameter estimates;
 call rannor(seed5,xnor5); call rannor(seed6,xnor6); call rannor(seed7,xnor7);
 brr=(96.7+xnor5*cv*96.7)*(1-exp(-(.051+xnor6*cv*.051)*(yb*100-
(31+xnor7*cv*31))));
 bhr=yb*brr/100;
 buckpop=bkill/bhr; doepop=buckpop*adsxratio;

*****Fawn:Doe Ratio;
 sight=fsight+dsight;
 call ranbin(seed4,sight,fsight/sight,xbin4);
 fawnsight=xbin4; if fawnsight=. then do; fawnsight=0; sight=0; end;
 doesight=sight-fawnsight;

fdratio=(fawnsight+lag&one(fawnsight)+lag&two(fawnsight)+lag&three(fawnsight)+la
g&four(fawnsight))/
(doesight+lag&one(doesight)+lag&two(doesight)+lag&three(doesight)+lag&four(doesi
ght));

*****Final Population Estimates;
 fawnpop=doepop*fdratio;
 prehuntpop=buckpop+doepop+fawnpop;
 prehuntdens=prehuntpop/area;
```

```
 loss=(bkill+dkill)*.15;
 posthuntpop=prehuntpop-bkill-dkill-loss;
 posthuntdens=posthuntpop/area;

output;
end;

proc univariate noprint;
 by dmu1 dmu2 yr;
 var posthuntpop posthuntdens;
 output out=stats1 cv=popcv pctlpre=P_ pctlpts=2.5,5,50,95,97.5;
 output out=stats2 p5=x D_5 median=x D_50 p95=x D_95;
 data last; merge stats1 stats2; by dmu1 dmu2 yr;
 data last1; merge one last; by dmu1 dmu2 yr;
  if yr<1990 then delete; if dmu='49B' and yr<1994 then delete;
  keep yr dmu1 dmu2 dmu popcv P_2_5 P_5 P_50 prehuntpop P_95 P_97_5
       D_5 D_50 prehuntdens D_95 posthuntpop posthuntdens;
  file 'E:\My Documents\Deer research\Wisconsin\posthunt estimates.txt';
  put yr dmu popcv P_5 posthuntpop P_95 D_5 posthuntdens D_95;
 proc print label noobs;
  label yr='Year' dmu='DMU' popcv='CV' prehuntpop='Preseason population size'
        prehuntdens='Preseason population density'
        posthuntpop='Postseason population density'
        posthuntdens='Postseason population density'
        p_2_5='Est Pop 2.5 percentile' p_5='90% LCL' p_50='Est Pop median'
            p_95='90% UCL' p_97_5='Est Pop 97.5 percentile'
            D_5='90% LCL' D_95='90% UCL';
  format D_5 prehuntdens posthuntdens D_50 D_95 popcv 5.1
         P_2_5 P_5 prehuntpop posthuntpop P_50 P_95 P_97_5 comma8.0;
  var yr dmu popcv P_5 posthuntpop P_95 D_5 posthuntdens D_95;

 run;
```